The Early Pleistocene ectothermic vertebrates of Pietrafitta (Italy) and the last Western European occurrence of *Latonia* Meyer, 1843

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Palaeobiology and palaeobiogeography of amphibians and reptiles — Jean-Claude Rage —

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ABSTRACT

The Early Pleistocene site of Pietrafitta (central Italy) produced a rich vertebrate assemblage from the Late Villafranchian Land Mammal Age (late MN18). Geological and paleobotanical data from Pietrafitta indicate a lacustrine environment, surrounded by a humid deciduous broadleaved forest with a temperate climate. The vertebrate assemblage consists of at least 40 taxa including actinopterygians, amphibians, reptiles, birds, and mammals. Here, we concentrate on the ichthyofaunal and herpetofaunal remains. The ichthyofauna includes *Barbus* Cuvier and Cloquet, 1816, *Scardinius* Bonaparte, 1837, aff. *Squalius* Cuvier, 1817, and *Tinca* Cuvier, 1817. The two anuran genera are the large-sized alytid frog *Latonia* Meyer, 1843 and the "green frog" *Pelophylax* Fitzinger, 1843. Three snake precloacal vertebrae were recognized, one attributed to Colubrines indet., another one to *Natrix* sp. Laurenti, 1768, and the largest and most complete vertebra is referred to the genus *Vipera s.l.* Laurenti, 1768 (cf. gr. "Oriental vipers"). The chelonian fossils, including some complete carapaces and plastrals, are attributed to the European pond turtle (*Emys* gr. *Orbicularis* Linnaeus, 1758) and Hermann's tortoise (*Testudo hermanni* Gmelin, 1789).

KEY WORDS
Pleistocene,
Villafranchian,
herpetofauna,
ichthyofauna,
Latonia,
Vipera.

RÉSUMÉ

Les vertébrés ectothermiques du Pléistocène inférieur de Pietrafitta (Italie) et la dernière occurrence européenne de Latonia *Meyer, 1843.*

Le site du Pléistocène inférieur de Pietrafitta (Italie centrale) a produit un riche assemblage de vertébrés de l'âge des mammifères terrestres du Villafranchien tardif (MN18 tardif). Les données géologiques et paléobotaniques de Pietrafitta indiquent un environnement lacustre, entouré d'une forêt humide de feuillus à feuilles caduques, au climat tempéré. L'assemblage de vertébrés comprend au moins 40 taxons dont des actinoptérygiens, des amphibiens, des reptiles, des oiseaux et des mammifères. Nous nous concentrons ici sur les restes de l'ichtyofaune et de l'herpétofaune. L'ichtyofaune comprend *Barbus* Cuvier & Cloquet, 1816, *Scardinius* Bonaparte, 1837, aff. *Squalius* Cuvier, 1817, et *Tinca* Cuvier, 1817. Les deux genres d'anoures sont la grenouille alyte de grande taille *Latonia* Meyer, 1843 et la « grenouille verte » *Pelophylax* Fitzinger, 1843. Trois vertèbres précloacales de serpent ont été reconnues, une attribuée à Colubrines indet., une autre à *Natrix* sp. Laurenti, 1768, et la plus grande et la plus complète vertèbre est référée au genre *Vipera s.l.* Laurenti, 1768 (cf. gr. « vipères orientales »). Les fossiles de chéloniens, dont quelques carapaces et plastrales complètes, sont attribués à la tortue d'étang européenne (*Emys* gr. *Orbicularis* Linnaeus, 1758) et à la tortue d'Hermann (*Testudo hermanni* Gmelin, 1789).

MOTS CLÉS
Pléistocène,
Villafranchien,
herpétofaune,
ichtyofaune,
Latonia,
Vipera.

INTRODUCTION

The Early Pleistocene locality of Pietrafitta has provided abundant vertebrate remains, representing one of the most productive paleontological sites of Italy. In the past six decades, a large number of bones of mammals, birds, reptiles, amphibians, and teleosts have been collected at Pietrafitta during the industrial exploitation of lignite mines. Although mammals and birds have received considerable attention (e.g. Mazza *et al.* 1993; Rustioni & Mazza 1993; Zucchetta *et al.* 2003; Gentili & Masini 2005; Cherin *et al.* 2018), the diversity and paleontological significance of the ectothermic vertebrates remain elusive. Here we provide the first comprehensive overview of the ectothermic vertebrates from Pietrafitta. The present paper is based on a large number of osteological remains of actinopterygians, amphibians, and reptiles that were collected

during the mining activities and are now housed in the "Museo Paleontologico Luigi Boldrini" in Pietrafitta. Actinopterygian remains document a poorly diversified assemblage that includes taxa still present in the Italian Peninsula. Conversely, the herpetofauna includes a variety of taxa of remarkable paleobiogeographic and paleoecological interest.

Beyond the "herpetofaunal stability hypothesis"

The so-called "herpetofaunal stability hypothesis" postulates that herpetofaunal taxa in Europe and North America underwent relatively few changes during the Pleistocene (Holman 1999; Bell *et al.* 2010). However, evidence shows that a progressive decline in herpetofaunal biodiversity took place in Europe during the Pliocene and the Early Pleistocene (Rage 2013; Blain *et al.* 2016). This decline, probably caused by the general harshening of the climatic conditions and the intensification of glaciation

pulses in the boreal hemisphere, led to the extirpation of several families of tropical reptiles and amphibians from Western Europe, including the Varanidae, Aniliidae *s.l.* Fitzinger, 1826, Elapidae Boie, 1827, Erycinae Bonaparte, 1831, and some Alytidae Fitzinger, 1843 (Bailon 1991; Bailon & Blain 2007; Blain *et al.* 2016). During the same period, the habitat of other groups became restricted to Southern Europe (e.g. Agamidae Gray, 1827, Anguidae Gray, 1825, Blanidae Kearney, 2003, "Oriental vipers", "Green Toads") (Blain *et al.* 2016; Villa & Delfino 2018; Blain & Bailon 2019). Several studies show how some Mediterranean areas acted as "sanctuaries" for thermophilous taxa that arrived from the northern regions of Europe around the Plio-Pleistocene boundary (Blain *et al.* 2016; Villa *et al.* 2018). The Italian Peninsula was well suited to become a refuge for these animals from the cooling climate trend that started in the Pliocene (about 3.0 Ma). During the early stages of the Early Pleistocene, northern and central Italy were characterized by a relatively constant humidity in both glacial and interglacial phases with forested wet habitats, whereas in the southern regions of the Peninsula the glacial phases saw drier conditions and open landscapes, which changed to sub-tropical and forested environments during the interglacial phases (Bertini & Sadori 2010; Villa *et al.* 2018). Paleobotanical studies suggest that the vegetation of central Italy shortly after the Plio-Pleistocene transition (Gelasian; 2.58-1.80 Ma) was particularly stable for a long time, as happened in central and western Europe during the previous stages (pre-Piancenzian). At the same time, in most other regions of Europe, the marked seasonality had important ecological consequences (Kahlke *et al.* 2011; Martinetto *et al.* 2014). This situation changed during the Calabrian (1.80-0.78 Ma), when a floral turnover reflected an alternation of temperate humid and drier cooler phases (Kahlke *et al.* 2011; Martinetto *et al.* 2014). The Pietrafitta vertebrate fossils have been collected from layers that accumulated during a temperate phase of this last stage. The fossil record of amphibians and reptiles of northern Italian sites shows how most of the taxa present during the Middle-Late Villafranchian (about 2.5-1.2 Ma) were similar, and in many cases identical, to those that inhabit the same areas today. This is not the case for most of the southern regions of the Peninsula, where taxa currently extirpated from the region persisted until the end of the stage (Villa *et al.* 2018). It is possible that the central and southern part of Italy acted as some sort of "trap" for these taxa that retreated to some refuge on the Peninsula, where they survived for a longer time interval, but got extirpated at a later stage because further migration was impossible due to the geographical barrier formed by the Mediterranean. Due to its geographical position, Pietrafitta could have acted as a refuge for these reptiles and amphibians that in other parts of continental Europe faced extirpation.

GEOLOGICAL AND PALEOENVIRONMENTAL SETTING

The Tavernelle-Pietrafitta sedimentary basin is located in central Italy, south of Lake Trasimeno, in the upper valley of
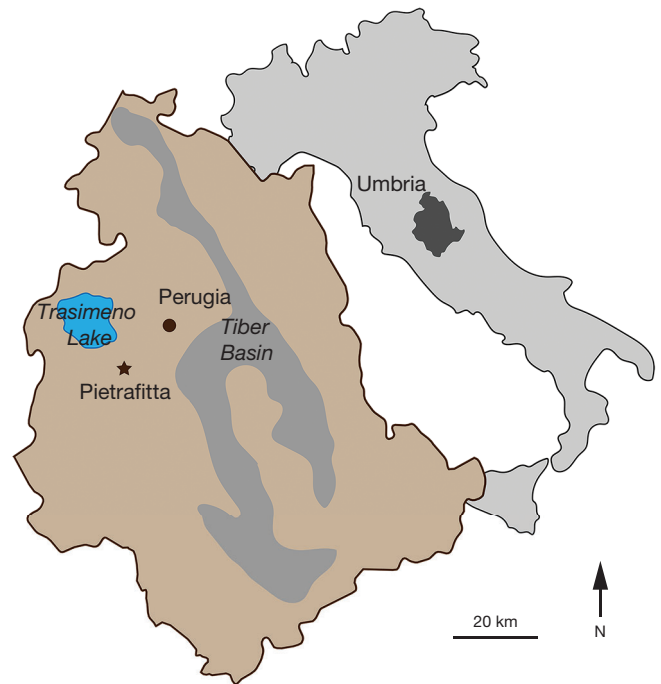
Fɪɢ. 1. — Location of the paleontological site of Pietrafitta within the Italian Peninsula.

the Nestore River, Umbria Region (42°59'33"N, 12°12'42"E) (Fig. 1). This small intermontane basin, which can be divided into two smaller basins (Tavernelle and Pietrafitta), extends in SW-NE direction for about 12 km, with a maximum width of about 5 km (Fig. 2). Because of intense tectonic activity, at least during some phases in the Early Pleistocene, it became part of a lateral branch of the main Tiber Basin, a large subsiding, tilting extensional basin on the western edge of the northern Apennine chain (Conti & Esu 1981; Ambrosetti *et al.* 1995; Cherin *et al.* 2012; Pazzaglia *et al.* 2013). During the Early Pleistocene, the Tavernelle-Pietrafitta Basin was characterized alternatively by lacustrine/palustrine and alluvial plain conditions. The elevation of the paleo-Nestore River delta driven by tectonic movements led to the formation of several small basins filled with freshwater (Conti & Girotti 1977; Conti & Esu 1981; Ambrosetti *et al.* 1987a, 1989). These palustrine environments represented the depositional contexts of the Pietrafitta lignite within the Pietrafitta basin.

According to the most recent geological mapping projects (Argenti *et al.* 2013), the deposits of the Tavernelle-Pietrafitta Basin are referred to the Nestore synthem, within the Tiberino supersynthem. The Nestore synthem is divided into two subsynthems: the lowermost Tavernelle subsynthem and the uppermost Pietrafitta subsynthem. The latter crops out near the homonymous village in the municipality of Piegaro, in the area where the industrial mining of lignite took place during the 20th century. The facies analysis performed on these deposits (which have a thickness varying between 6 and 12 m) indicates the presence of a marshy and humid area with abundant organic production and fine clastic sedimentation. Therefore, the lignite was probably deposited in a swampy

TABLE 1. — List of vertebrates (in alphabetical order) from Pietrafitta (Italy), modified from Argenti (2004), Zucchetta *et al.* (2003), Pandolfi *et al.* (2017), and Cherin *et al.* (2018).

Vertebrates from Pietrafitta (Italy)
Ichthyofauna
Tinca sp.
Scardinius cf. *erythrophthalmus* Linnaeus, 1758
aff. *Squalius*
Barbus sp
Herpetofauna
Latonia sp.
Pelophylax sp.
Emys gr. *orbicularis* Linnaeus, 1758
Testudo hermanni Gmelin, 1789
Natrix sp.
Colubrines indet.
Vipera (*s.l.*) sp. (cf. gr. "Oriental vipers")
Avifauna
Anas crecca/querquedula Linnaeus, 1758
Anas sp.
Aythya sp.
cf. *Gallus*
cf. *Ixobrychus*
Cygnus sp.
Phalacrocorax sp.
Podiceps sp.
Rallidae indet.
Somateria aff. *mollissima* Linnaeus, 1758
Mammalofauna
Acinonyx pardinensis Croizet & Jobert, 1828
Castor fiber plicidens Major, 1874
Equus sp.
Eucladoceros sp.
Leptobos aff. *vallisarni* Merla, 1949
Macaca sylvana florentina Cocchi, 1872
Mammuthus meridionalis Nesti, 1825
Praemegaceros obscurus (Azzaroli, 1953)
Microtus (*Allophaiomys*) cf. *chalinei* Alcalde, Agustí & Villalta, 1981
Microtus (*Allophaiomys*) cf. *ruffoi* Pasa, 1947
Mimomys pusillus Jànossy & van der Meulen, 1975
Oryctolagus cf. *lacosti* Pomel, 1853
Pannonictis nestii Martelli, 1906
Pseudodama farnetensis Azzaroli, 1992
Sciurus sp.
Sorex cf. *minutus* Linnaeus, 1766
Stephanorhinus etruscus (Falconer 1868)
Talpa sp.
Ursus etruscus Cuvier, 1823

area located on the edge of a lake (Conti & Girotti 1977; Ambrosetti *et al.* 1987b, 1992, 1995; Martinetto *et al.* 2014). The lignite deposit bears layers of organic clay with clasts, freshwater mollusks (Ambrosetti *et al.* 1992), and oligohaline ostracods (Gliozzi *et al.* 1997). The occurrence of these thin layers is probably related to high-energy events, such as storms, which remobilized the sediment of the lake bottom towards the marginal swamp (Pazzaglia 2007). At the end of the Early Pleistocene, the tectonic uplift led to the progressive desiccation of the basin (Argenti 1999).

The lignite deposits cropping out at Pietrafitta have been known in the scientific literature since the first half of the 20th century (e.g. Ugolini 1921; Moretti 1949), but they had already been exploited for domestic use since the 19th century.

The industrial mining of lignite to feed the nearby thermoelectric power plant continued from the 1930s to the 1980s. In 1966, the assistant head miner Luigi Boldrini, while inspecting the excavations of the lignite deposit, began to set up the first paleontological collection at Pietrafitta. However, only in the 1980s, the Archaeological Department of Umbria and the University of Perugia started the systematic collection of fossil findings, now stored in the "Museo Paleontologico Luigi Boldrini" in Pietrafitta (Gentili *et al.* 2000; Martinetto *et al.* 2014).

The particular depositional and environmental conditions of the swamp allowed the preservation of a rich assemblage of fossil vertebrates, other metazoans, and plants. The vertebrate assemblage is biochronologically referred to around 1.5 Ma, which is referred to the Farneta Faunal Unit (FU) of the Late Villafranchian Land Mammal Age, corresponding to the late MN18 of the European Mammal Biochronology scheme (Torre *et al.* 1992; Gliozzi *et al.* 1997; Gentili *et al.* 2000; Rook & Martínez-Navarro 2010).

Fossil plants and pollen of Pietrafitta confirmed previous paleoenvironmental reconstruction of a palustrine assemblage. The flora was dominated by aquatic genera such as *Azolla* Lamarck, 1783, *Najas* Linnaeus, 1753, *Nymphaea* Linnaeus, 1753, and *Potamogeton* Linnaeus, 1753 (Martinetto *et al.* 2014), and is generally characterized by a remarkable diversity, including exotic genera still living in other regions today (e.g. *Azolla*, *Decodon* Gmelin, 1721, *Euryale* Salisbury, 1805), as well as extinct species of Eastern European affinity (e.g. *Cyperus glomeratoides* Velichkevich & Zastawniak, 2003, *Nymphaea borysthenica* Dorofeev, 1974, *Potamogeton pannosus* Dorofeev, 1974) (Martinetto *et al.* 2014). The lack of sedimentological evidence of transport and the presence of root remains indicate that the plants were preserved *in situ*. The palynological study shows a consistent diversity of the flora living in the surroundings of the swamp during the time interval in which the lignite accumulated (Lona & Bertoldi 1972; Martinetto *et al.* 2017). The lower horizons were marked by the dominance of *Taxodium*-type pollen, which suggest a warm-temperate "subtropical" climate (Kottek *et al.* 2006). Subsequently, the so-called "Tiberian boundary" (Lona & Bertoldi 1972), currently considered devoid of any chronological relevance (Bertini & Sadori 2010), is marked by the disappearance of the *Taxodium*-type pollen. From this horizon onwards, "*Quercetum*" taxa prevail and indicate a warm temperate climate characterized by a mixed deciduous forest (Kottek *et al.* 2006). The upper horizons are dominated by herbaceous pollen and *Pinus* Linnaeus, 1753, which are typical of cooler climate phases with open vegetation and conifer forests (Kottek *et al.* 2006). The vertebrate-bearing lignite layers were initially deposited in an environment characterized by humid and temperate climate, in which the paleolake was surrounded by broad leaved deciduous forest (Martinetto *et al.* 2014). The vertebrate fossil remains from these layers are very abundant and represent a high diversity of taxa, including actinopterygians, amphibians, reptiles, birds, and mammals (Kotsakis & Gregori 1985; Argenti
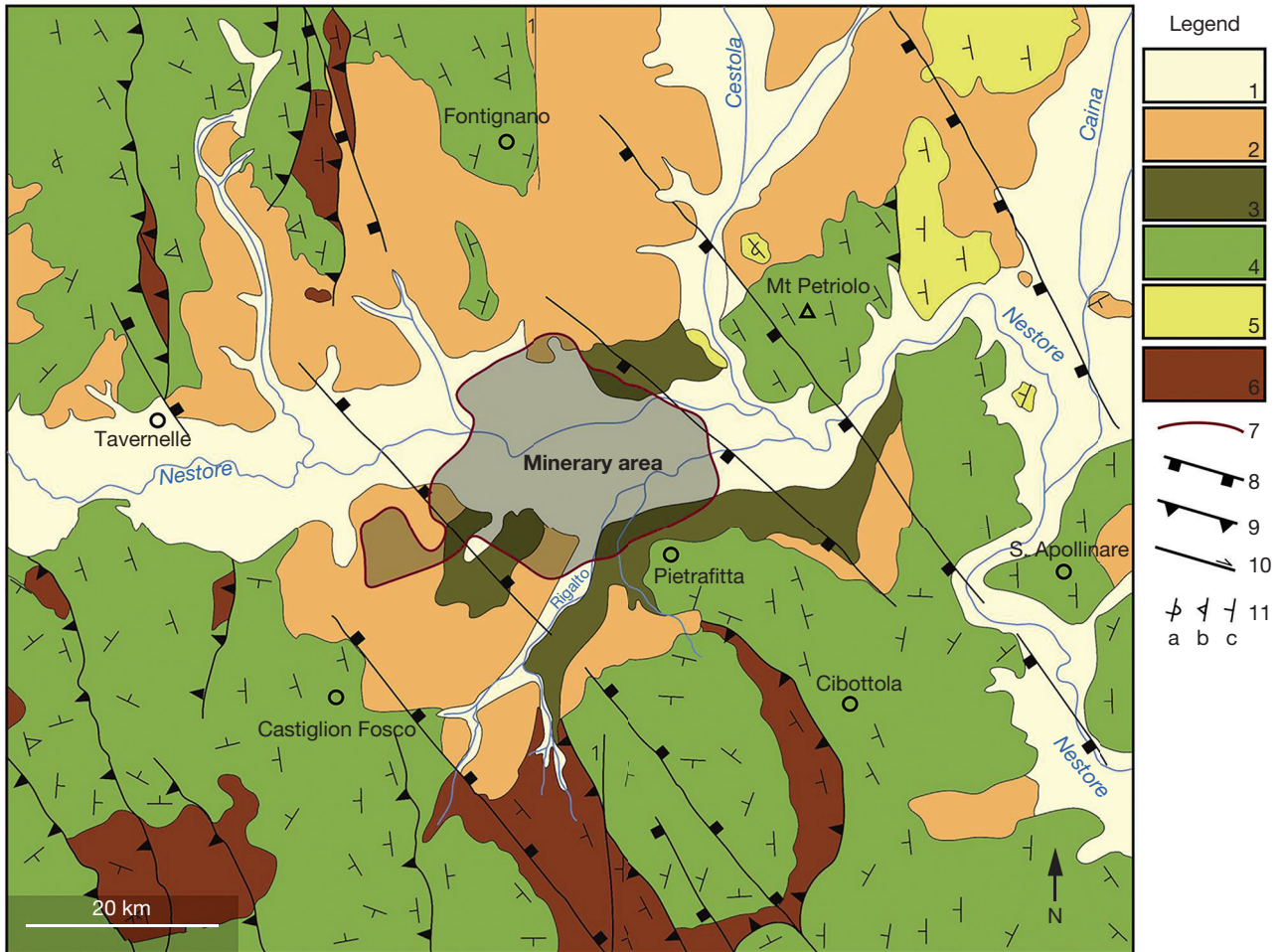
Fig. 2. — Structural and geological map of the Pietrafitta-Tavernelle area, modified from Menichetti (1997): **1**, recent alluvium; **2**, lacustrine deposits of the Tavernelle basin; **3**, lacustrine deposits of the Pietrafitta basin; **4**, "Marnosa umbra" and "Marnoso arenacea" Formations; **5**, trasimeno sandstone; **6**, varicolored mélange; **7**, original volume of the lignite seam before the mining activity; **8**, extensional faults (the indentations show the hanging-wall); **9**, reverse and thrust faults (the triangles show the hanging-wall); **10**, strike slip faults; **11**, attitude of the strata (**a**, overturned; **b**, dip <45°; **c**, dip >45°).

1999; Delfino 2002; Zucchetta *et al.* 2003; Barisone *et al.* 2006; Argenti & Kotsakis 2009; Martinetto *et al.* 2014). The collection comprises more than 2.000 fossils belonging to at least 40 taxa (Table 1). The lack of systematic research effort has led to a known assemblage artificially biased in favor of large mammals, which, due to this, clearly predominate over the small vertebrate remains. The organisms were presumably accumulated after death near their habitat. The skeletons of some large mammals were found in their original anatomical position or slightly scattered without significant evidence of prolonged floating (Ambrosetti *et al.* 1992).

MATERIAL AND METHODS

The material described herein includes 826 ichthyofaunal and herpetofaunal remains from the Pietrafitta site excavated during the 1980s and 1990s, formerly by the head miner Luigi Boldrini and, later, by the Archaeological Department of Umbria with the support of the Department of Earth Sciences of the University of Perugia. All the fossils are housed in the "Museo Paleontologico Luigi Boldrini", Pietrafitta. The fossil specimen numbers in the text may include more than one element.

The anatomical nomenclature mostly follows Rutte (1962) for fishes, Roček (1994) and Biton *et al.* (2016) for anurans, Zangerl (1969) for turtles, and Szyndlar (1984) for snakes. Selected fish, anuran, and snake specimens were drawn by hand and edited using the software Adobe Photoshop CC and Adobe Illustrator CC 2015. Selected chelonian specimens were photographed using CANON POWERSHOT G7X and NIKON D750 cameras.

INSTITUTIONAL ABBREVIATIONS

MDHC — Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino;

NNHC-HUJ — National Natural History Collection, Hebrew University of Jerusalem;

PFHER — Pietrafitta herpetofaunal remains, Museo Paleontologico "Luigi Boldrini" di Pietrafitta;

PFICT — Pietrafitta ichthyofaunal remains, Museo Paleontologico "Luigi Boldrini" di Pietrafitta.

SYSTEMATIC PALEONTOLOGY

Infraclass TELEOSTEI Müller, 1845
Order CYPRINIFORMES Bleeker, 1859
Family CYPRINIDAE Bonaparte, 1837
Genus *Barbus* Cuvier & Cloquet, 1816

Barbus sp.
(Fig. 3)

REFERRED MATERIAL. — PFICT0005: 25 isolated partially complete unbranched dorsal-fin rays (Fig. 3A).

DESCRIPTION
The available material consists of robust and heavily ossified unbranched dorsal-fin rays characterized by a remarkable serration along their posterior margin (Fig. 3A-C). The serrae are closely spaced and are usually restricted to the distal half of the ray. The mesial side of the ray is marked by a robust ridge associated with a delicate, very shallow longitudinal groove.

REMARKS
All the 25 examined specimens exhibit a very similar morphology and likely represent the posterior (third) unbranched dorsal-fin ray of a cyprinid fish. As reported by Howes (1987), a serrated unbranched dorsal-fin ray occurs in selected species of the genera *Barbus*, '*Puntius*' Hamilton, 1822, *Schizothorax* Heckel, 1838, and *Mystacoleucus* Günther, 1868, and in all the species of the genera *Acrossocheilus* Ōshima, 1919, *Cyclocheilichthys* Bleeker, 1879, and *Cyprinus* Linnaeus, 1758. The overall morphology of the rays documented herein is very similar to those characteristics of certain species of the genus *Barbus* (e.g. Přikryl *et al.* 2016), including the extant Italian species *B. plebejus* Bonaparte, 1839 and *B. tyberinus* Bonaparte, 1839 (Kottelat & Freyhof 2007). Consequently, we refer PFICT0005 to *Barbus* sp.

Genus *Scardinius* Bonaparte, 1837

Scardinius cf. *erythrophthalmus* Linnaeus, 1758
(Fig. 3)

REFERRED MATERIAL. — PFICT00003: 13 isolated moderately to poorly preserved pharyngeal teeth (Fig. 3D-G).

DESCRIPTION
The teeth are slender with a high and laterally compressed crown and a notably constricted neck (Fig. 3B, C). The masticatory surface is strongly oblique, forming an angle of more than 70° with the main axis of the tooth. There are up to seven or eight delicate spinous or knob-like tubercles separated from each other by marked furrows along the inner side of the masticatory surface. The distal tip of each tooth is characterized by a moderately to well-developed hook. The outer side of the crown is smooth.

Based on the number of tubercles on the masticatory surface and overall configuration of the transition between crown and neck, it is possible to recognize two morphotypes. The teeth pertain-ing to the first morphotype (A) (Fig. 3D, E) have less numerous (four to six) tubercles and a visible bending in the proximity of the transition between the crown and the neck to the teeth and possibly correspond to the second or third element of the main row of the pharyngeal bone, corresponding to the position 4 or 5 of the classificatory system proposed by Rutte (1962). The teeth of the second morphotype (B) (Fig. 3F, G) show seven or eight tubercles on the masticatory surface, a strongly developed hook and a nearly vertical posterior side of the crown. These teeth possibly represent the penultimate or last elements of the main row of the pharyngeal bone, corresponding to the position 2 or 3 of the classificatory system proposed by Rutte (1962).

REMARKS
All the 13 documented teeth were extracted from lignite slabs associated with extensively damaged and unidentifiable cranial and post-cranial bones. The overall morphology of the teeth with a hooked distal tip and the presence of knob-like tubercles along the inner side of the masticatory surface justify the attribution to the genus *Scardinius* (e.g. Rutte 1962). The number of knob-like tubercles and the remarkably constricted neck point to the extant rudd *S. erythrophthalmus* to which we tentatively refer these specimens (e.g. Obrhelová 1970a; Miranda & Escala 2002).

Genus *Squalius* Cuvier, 1817

aff. *Squalius*
(Fig. 3)

REFERRED MATERIAL. — PFICT00004: 14 isolated poorly preserved pharyngeal teeth (Fig. 3H, I).

DESCRIPTION
The teeth are stout with a relatively low crown and a large neck (Fig. 3). The masticatory surface is considerably bent, narrow, and slightly depressed, bearing two small central tubercles. The hook is usually well developed, blunt, and robust.

REMARKS
The overall morphology of the teeth, with a very large neck that exceeds crown width, a blunt and large hook, and a narrow masticatory surface are reminiscent of those of certain species of the genus *Squalius*, especially *S. cephalus* (Linnaeus, 1758) (see Rutte 1962). However, the poor preservation of the available material does not allow to refer them to any taxon more specific than aff. *Squalius*.

Genus *Tinca* Cuvier, 1817

Tinca sp.
(Fig. 4)

REFERRED MATERIAL. — PFICT00001: 64 isolated and moderately preserved pharyngeal teeth; PFICT00002: 4 pharyngeal bones with articulated teeth (Fig. 4A-H).
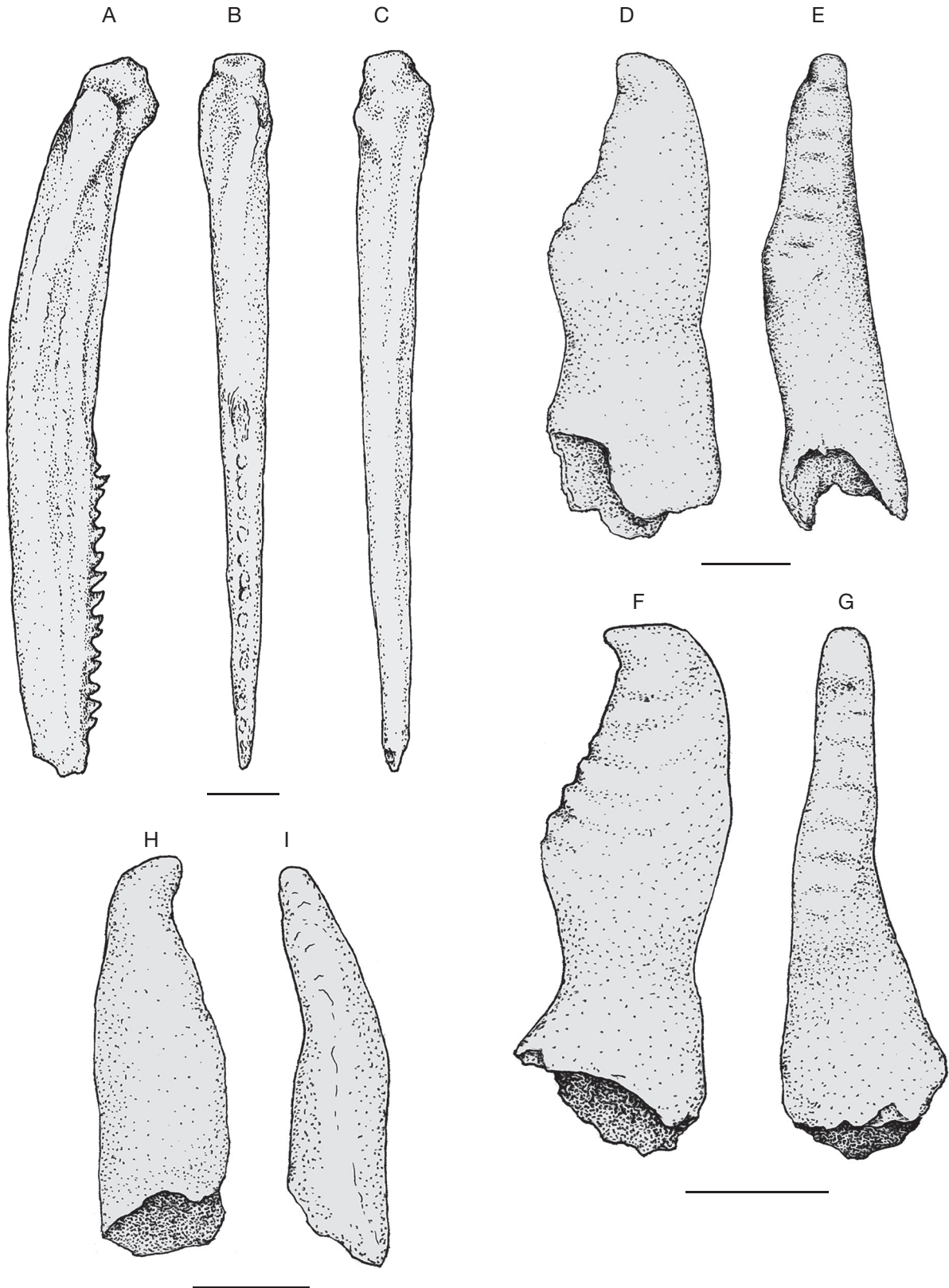
Fɪɢ. 3. — *Barbus* sp.: **A**-**C**, serrated spine (PFICT0005) in lateral (**A**), dorsal (**B**), and frontal (**C**) views; **D**, **E**, *Scardinius* cf. *erythrophthalmus*: pharyngeal tooth, morphotype A (PFICT00003) in lateral (**D**) and frontal (**E**) views; **F**, **G**, pharyngeal tooth, morphotype B (PFICT00003) in lateral (**F**) and frontal (**G**) views; aff. *Squalius*: **H**, **I**, pharyngeal tooth, (PFICT00004) in lateral (**H**) and frontal (**I**) views. Scale bars: 1 mm.

DESCRIPTION

The teeth are robust, stout, and blunt. The crown is nearly oval in cross section with a convex outer surface. The masticatory surface is inclined forming an angle of 50-60° with the main axis of the tooth in the majority of the specimens. The pharyngeal bones are distinctly curved and bear four or five teeth with different morphology, which are arranged in a single row. Overall, five morphotypes seem to be recognizable among the available material.

The teeth of the first morphotype (A) are tear-shaped and characterized by a hook that emerges from the posterior edge of the crown (Fig. 4A). The tip of the hook is posterolaterally oriented. A small curved incision extends along the masticatory surface of the tooth.

The teeth of the second morphotype (B) are characterized by a less pronounced hook-like structure compared to the state in morphotype A (Fig. 4B, C). The anterolateral surface of the teeth is convex. There is a small sinuous incision extending along the masticatory surface, and a small bulge next to it on the anterolateral side.

The teeth of the third morphotype (C) are characterized by a nearly spherical crown (Fig. 4D). The hook is vertically oriented. In general, the masticatory surface is marked by a small depression.

The crown of the teeth of the fourth morphotype (D) exhibits a small and rounded hook-like process and a short incision (Fig. 4E, F).

The teeth of the fifth morphotype (E1, E2) (Fig. 4G, H) have a considerably steep to nearly vertical masticatory surface with a central hook-like process in E2 (Fig. 4H). Small lateral bulges and furrows can be also observed.

REMARKS

The morphology of the teeth and the overall structure of the pharyngeal bones are consistent with those of the genus *Tinca* (e.g. Rutte 1962). Both the teeth and the pharyngeal bones appear to be very similar to those of the extant green tench *Tinca tinca* (Linnaeus, 1758) (e.g. Obrhelová 1970b; Miranda & Escala 2002). However, it is not possible to provide an unambiguous assignment at species level due to the poor preservation of the available material and the limited number of traits useful for taxonomic discrimination.

Class AMPHIBIA Linnaeus, 1758
Order ANURA Fischer von Waldheim, 1813
Family ALYTIDAE Fitzinger, 1843
Subfamily DISCOGLOSSINAE Günther, 1858
Genus *Latonia* Meyer, 1843

Latonia sp.
(Figs 5-8)

REFERRED MATERIAL. — PFHER00012: 1 Premaxilla; PFHER00004A, PFHER00004B, PFHER00040A, PFHER00040B: 4 maxillae; PFHER00018, PFHER00034A, PFHER00034B, PFHER00034C: 4 fragments of frontoparietals; PFHER00010A, PFHER00010B: 2 pterygoids; PFHER00020A, PFHER00020B, PFHER00023, PF-

HER00043: 4 prootico-occipitals; PFHER00003A, PFHER00003B, PFHER00025, PFHER00039: 4 prearticulars; PFHER00026: 1 atlas; PFHER00037: 1 presacral vertebra; PFHER00017: 15 fragmentary vertebrae; PFHER00008, PFHER00036: 2 urostyles; PFHER00019A, PFHER00019B, PFHER00032A, PFHER00032B, PFHER00032C, PFHER00032D, PFHER00097: 7 ribs; PFHER00009, PFHER00028A, PFHER00028B: 3 scapulae; PFHER00013A, PFHER00013B, PFHER00027, PFHER00044: 4 coracoids; PFHER00014A, PFHER00014B: 2 clavicles; PFHER00002A, PFHER00002B, PFHER00035A, PFHER00035B: 4 humeri; PFHER00007, PFHER00033, PFHER00046: 3 radioulnae; PFHER00005A, PFHER00005B, PFHER00029, PFHER00047A, PFHER00047B: 5 ilia; PFHER00015: 1 ischium; PFHER00038A, PFHER00038B, PFHER00071A, PFHER00071B: 4 femora; PFHER00001A, PFHER00001B, PFHER00041A, PFHER00041B, PFHER00041C, PFHER00041D: 6 tibiofibulae; PFHER00011, PFHER00022A, PFHER00022B, PFHER00030, PFHER00042A, PFHER00042B: 6 tarsals; PFHER00021, PFHER00024, PFHER00045: 20 indeterminate elements (Figs 5-8).

DESCRIPTION

These fossils belong to at least three different individuals, the bones of which were found associated. One of the individuals is characterized by a larger size compared to the other two. This may be due to sexual dimorphism or a different individual age of the animals.

The premaxilla (Fig. 5A, B) is characterized by a short *pars facialis*, with a deep recess on the inner side. A visible depression (*recessus marsupiatus sensu* Roček 1994) marks the base of the *pars facialis* in external view. The maxillae (Fig. 5C, D) have a smooth lateral surface without any ornamentation. Most of the maxillae do not preserve the teeth but only their peduncles. When present, the teeth show typical anuran features: they are monocuspid, pedicellated, pleurodont, and densely packed, curved, and pointed. It is possible to estimate the maximum number of maxillary tooth positions to about 65. The tooth row extends slightly posterior to the *lamina horizontalis*. The internal surface of the maxilla is marked by a wide, depressed area below the zygomatic-maxillary process (posterior depression *sensu* Roček 1994). The *processus zygomatico-maxillaris* is long, horizontal and has a straight dorsal margin. The pterygoid process is large and extended both caudally and medially. Although fragmentary, the best-preserved frontoparietals (Fig. 5E, F) preserve two distinct portions of the anterior section and part of the posterior section, including each *canthus postero-lateralis*. Dorsally, the two anterior sections have a strongly ornamented surface. The dermal ornamentations consist in small tubercles that fuse with one another anterolaterally, forming short, irregular ridges. The posterior parts present well-developed *canthi postero-lateralis* and a rather high medial crest between them. The two pterygoids are incomplete. The most complete specimen preserves the main body, the ventral flange, and the ramus anterior (Fig. 5G, H). The ventral flange (*dilatatio alaris* in Biton *et al.* 2016) of both pterygoids is well developed and bears visible rugosities on the dorsal surface. A deep groove extends along the ramus anterior above the ventral flange. The prootico-occipital (Fig. 6A-D) is large but slender, increasing in width toward the distal part of the *crista parotica*.
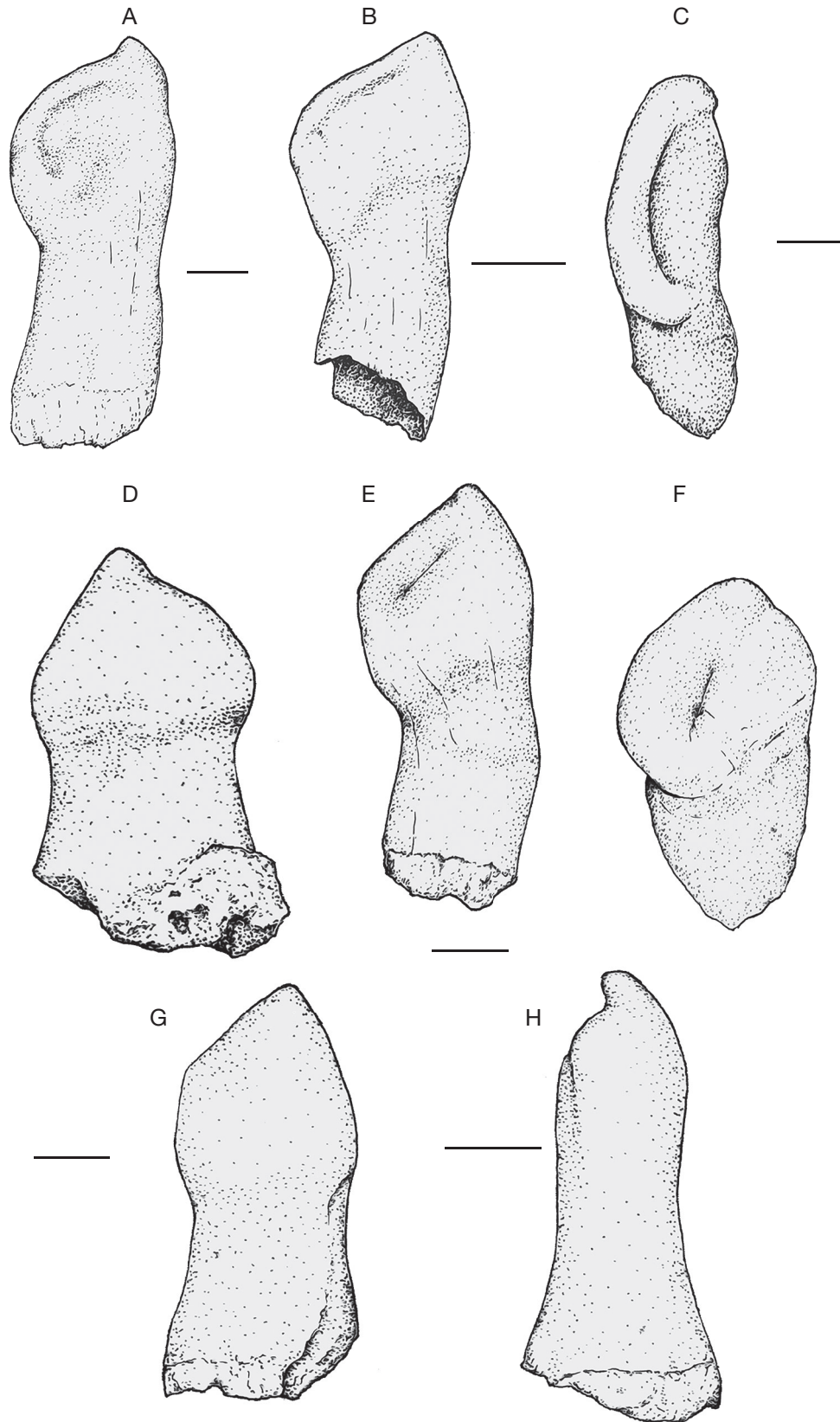
FIG. 4. — *Tinca* sp.: **A**, pharyngeal tooth, morphotype A (PFICT00001) in lateral view; **B**, **C**, pharyngeal tooth, morphotype B (PFICT00001) in lateral (**B**) and dorsal (**C**) views; **D**, pharyngeal tooth, morphotype C (PFICT00003) in lateral view; **E**, **F**, pharyngeal tooth, morphotype D (PFICT00001) in lateral (**E**) and dorsal (**F**) views; **G**, pharyngeal tooth, morphotype E1 (PFICT00001) in lateral view; **H**, pharyngeal tooth, morphotype E2 (PFICT00001) in lateral view. Scale bars: 1 mm.
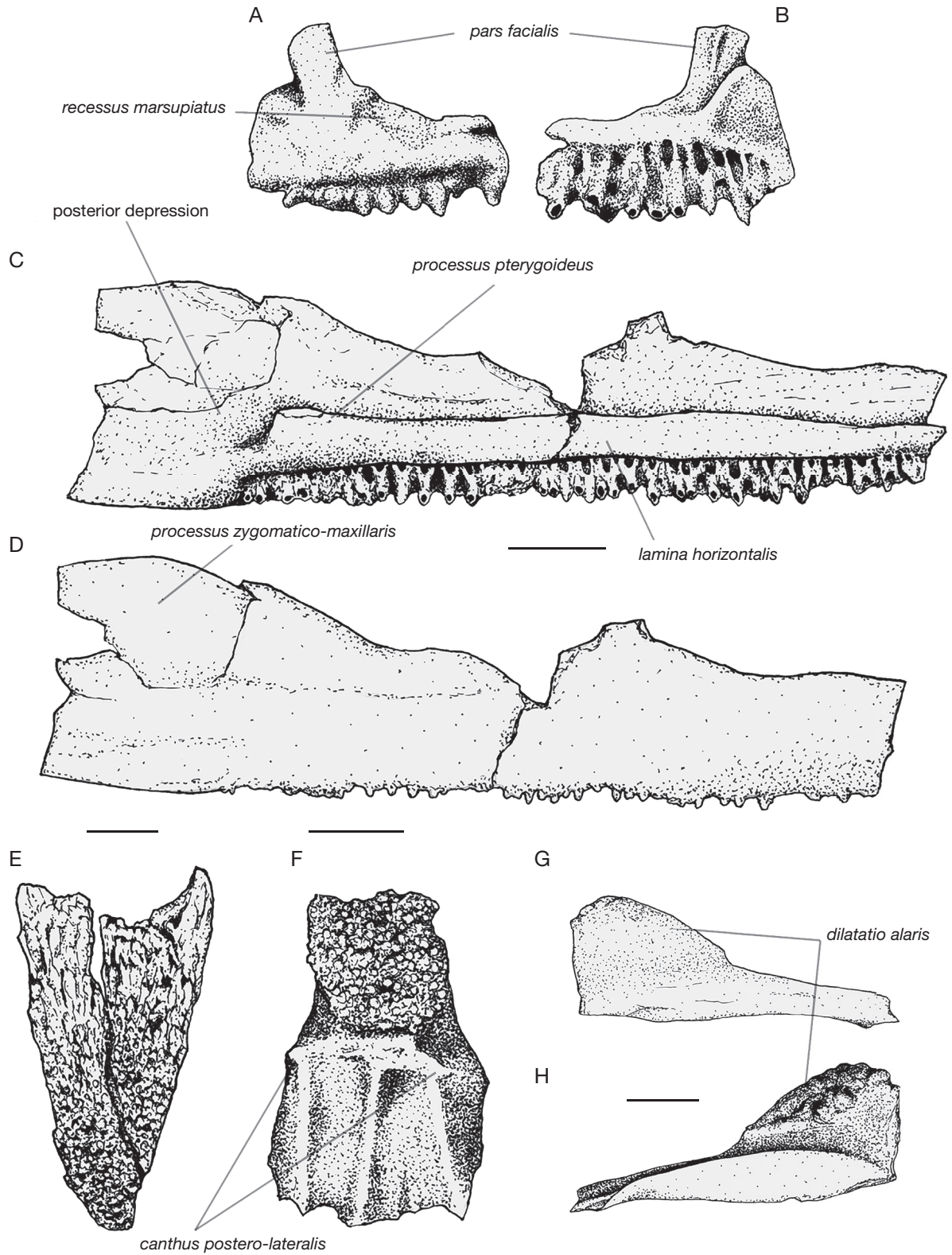
Fig. 5. — *Latonia* sp.: **A**, **B**, right premaxilla (PFHER00012) in anterior (**A**) and posterior (**B**) views; **C**, **D**, left maxilla (PFHER00040A) in medial (**C**) and lateral (**D**) views; **E**, **F**, fragments of frontoparietal (PFHER00034A, PFHER00034B) in dorsal views; **G**, **H**, left pterygoid (PFHER00010A) in ventral (**G**) and dorsal (**H**) views. Scale bars: 3 mm.
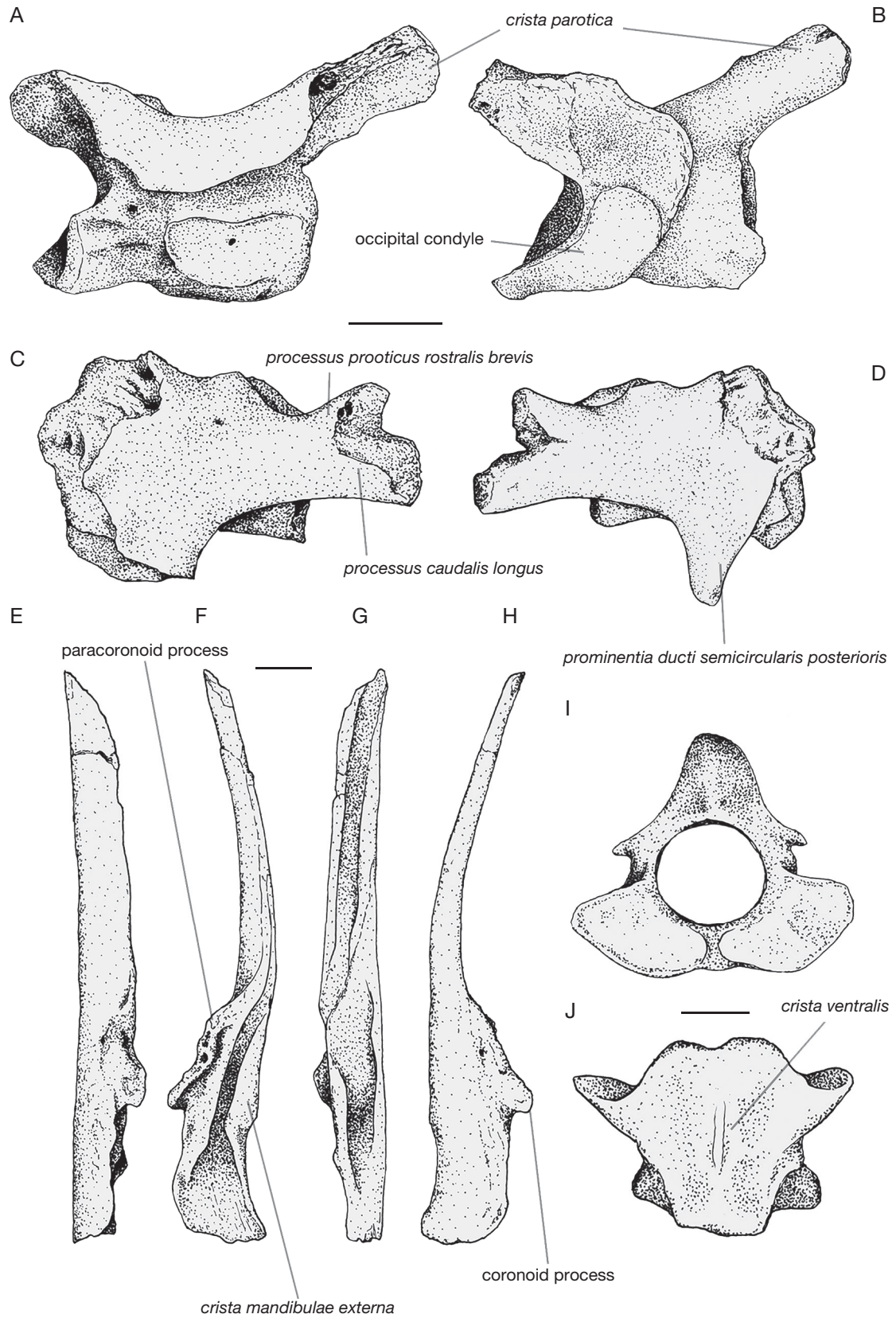
FIG. 6. — *Latonia* sp.: **A**-**C**, left prootico-occipital (PFHER00020B) in anterior (**A**), posterior (**B**), and dorsal (**C**) views; **D**, right prootico-occipital (PFHER00043) in dorsal (**D**) view; **E**-**H**, right prearticular (PFHER00025) in medial (**E**), dorsal (**F**), lateral (**G**), and ventral (**H**) views; **I**, **J**, atlas (PFHER00026) in anterior (**I**) and ventral (**J**) views. Scale bars: 3 mm.

The latter is bifurcated into two processes: a shorter anterior process (*processus prooticus rostralis brevis*) and a longer posterior one (*processus caudalis longus*). The contact area for the frontoparietal is striated. The occipital condyle is rather prominently surmounted by the *prominentia ducti semicircularis posterioris* (*sensu* Roček 1994), which is long, laminar and bears a ventral extension that reaches and, in one specimen (PFHER00043), exceeds the occipital condyle in posterior and dorsal view. All the recovered prearticulars (Fig. 6E-H) have both an anterior paracoronoid process and a posterior coronoid process. The lateral surface of this bone has a deep depression that extends longitudinally above the sharp *crista mandibulae externa*.

The centrum of the atlas (Fig. 6I, J) is dorsoventrally compressed. It has a posterior subcircular cotyle. The two anterior cotyles, complementary to the occipital condyles, are not confluent (cotylaric type II of Lynch 1969). The ventral median crest (*crista ventralis*) on the ventral surface of the vertebral body is very distinct. The posterior edge of the neural arch bears a short neural spine. The only well-preserved non-atlas presacral vertebra (PFHER00037) is in relatively good condition even if the distal portions of the transverse processes are missing. The vertebra is opisthocoelous and has stout transverse processes that are orientated posteriorly. The neural crest, which is well marked, has a pointed posterior end. All ribs show enlarged ends and a constricted middle portion. In the largest rib (Fig. 7A), a hooked process arises from the thinnest part of the bone. The short and robust scapulae (Fig. 7B) are incomplete and poorly preserved. They display a thin lamina (*tenuitas cranialis sensu* Roček, 1994) along the anterior margin. In all coracoids (Fig. 7C), the *pars glenoidalis* is moderately large and slightly flattened or subrounded in cross section, whereas the *pars epicoracoidealis* is almost laminar. The main body is strongly curved, with a constriction in the middle portion. The clavicles (Fig. 7D) are slender and bent. The urostyle (Fig. 7E-G) has two cotyles anteriorly. The neural arch of this element bears a pair of short transverse processes with flat ends. The best-preserved humerus (Fig. 7H, I) appears to be curved, with a lateral concavity. A well-developed *crista ventralis* is present in all humeri and flanked by a less marked *crista paraventralis*. The *eminentia capitata* is spherical and laterally shifted, flanked by a large *epicondylus ulnaris* and a smaller *epicondylus radialis*. The *crista medialis* is moderately developed, whereas the *crista lateralis* is very low. The radioulnae (Fig. 7J) are elongated and of large size. They have a large proximal portion and a flattened distal end. On the distal epiphysis, the radial component is slightly larger than the ulnar part. The most-complete ilia (Fig. 8A-E) clearly show a *crista dorsalis*, an elongated *tuber superior*, an elongated and pointed *pars ascendens*, and a slightly reduced *pars descendens*. The *crista dorsalis* is moderately high and bends medially. Medially, there is a deep interiliac groove, but the interiliac tubercle is strongly reduced in most of the specimens. Underneath the tuber superior, a small but deep depression (*fossula tuberis superioris*) is distinguishable and a shallow supracetabular fossa is present posterior to the tuber. The femur (Fig. 8F, G) is sigmoid and has a low but evident *crista femoris*. In the tibiofibulae (Fig. 8H, I), the concave lateral margin is characterized by the presence of a small but relatively sharp *crista cruris*. Both the sulcus distalis and the *sulcus proximalis* are deep. At the epiphyses, the elliptical ends of both tibial and fibular components have parallel main axes. The astragalus and the calcaneum are not fused, with the former being larger than the latter.

REMARKS
The large anuran represented by these fossil remains shows a combination of features that is clearly diagnostic for the alytid genus *Latonia*, among which a premaxilla with a deep recessus on the inner surface of the pars facialis; a wide medial depression in the posterior part of the maxilla; a long, horizontal processus zygomaticus-maxillaris with a straight dorsal margin; the presence of two distinct processes on the prearticular (*processus paracoronoideus* and *processus coronoideus*); a clear depression located on the posterior part of the lateral surface of the same bone, above the *crista mandibulae externa*; a pterygoid with a well-developed ventral flange; a ventral keel on the atlas; a laterally-shifted *eminentia capitata*; an ilium with a *crista dorsalis* and a prominent *pars ascendens*; and unfused astragalus and calcaneum, which differ in size (Roček 1994, 2013; Biton *et al.* 2013, 2016).

Within *Latonia*, the presence/absence of ornamentation on the lateral surface of the maxilla is considered one of the most important characters for the specific attribution, even though it is not the only diagnostic feature. The Pietrafitta *Latonia* has no trace of ornamentation on the maxillae. Roček (1994: 724) noticed that this ornamentation is separated from the compact bone of the underlying jaw by an irregularly perforated bone tissue that can easily cause the separation of the ornamentation from the maxilla itself. However, given the absence of any trace of ornamentation or fractures on the bone, it seems unlikely that the maxillae from Pietrafitta have lost the ornamentation for taphonomic reasons (e.g. removed by water fluxes or movements of the remains during deposition). Among the five currently accepted species of *Latonia* (*Latonia seyfriedi* Meyer, 1843, *L. caucasica* Syromyatnikova & Roček, 2019, *L. ragei* Hossini, 1993, *L. vertaizoni* Friant, 1944, and the extant *L. nigriventer* (Mendelssohn & Steinitz, 1943); Roček 1994, 2013; Biton *et al.* 2016; Syromyatnikova & Roček 2019; Syromyatnikova *et al.* 2019; Villa *et al.* 2019), this absence distinguishes the Pietrafitta taxon from *L. seyfriedi* (which includes *L. gigantea* (Lartet, 1851) as a junior synonym, according to Syromyatnikova *et al.* 2019), which have ornamented maxillae (Roček 1994, 2013; Syromyatnikova & Roček 2019; Syromyatnikova *et al.* 2019). However, the other four species (*L. caucasica*, *L. nigriventer*, *L. ragei*, and *L. vertaizoni*) have smooth maxillae (Hossini 1993; Roček 1994, 2013; Biton *et al.* 2016; Syromyatnikova & Roček 2019), like the Pietrafitta specimens.

In addition, the Pietrafitta *Latonia* shows some peculiar features that are not presently reported in any of the known species of the genus, irrespectively of them having smooth or ornamented maxillae. First, the Italian fossils bear distinct rugosities on the ventral flange of the pterygoids.
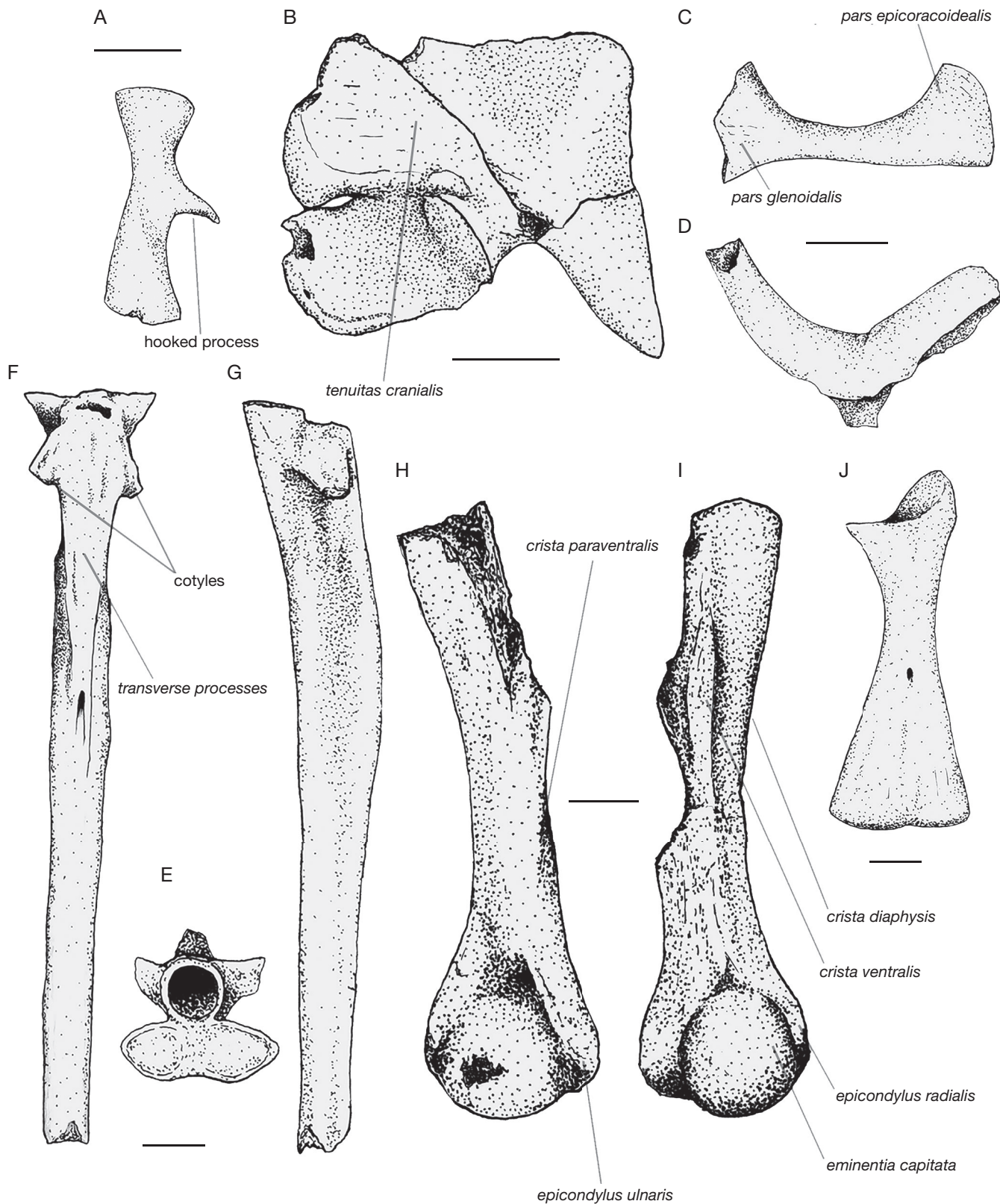
FIG. 7. — *Latonia* sp.: **A**, rib (PFHER00019A); **B**, left scapula (PFHER00009) in external view; **C**, left coracoid (PFHER00013A) in dorsal view; **D**, right clavicle (PFHER00014B) in dorsal view; **E-G**, urostyle (PFHER00008) in dorsal (**E**), lateral (**F**), and anterior (**G**) views; **H**, **I**, left humerus (PFHER00035B) in dorsal (**H**) and ventral (**I**) views; **G**, left radioulna (PFHER00033) in lateral view. Scale bars: 3 mm.
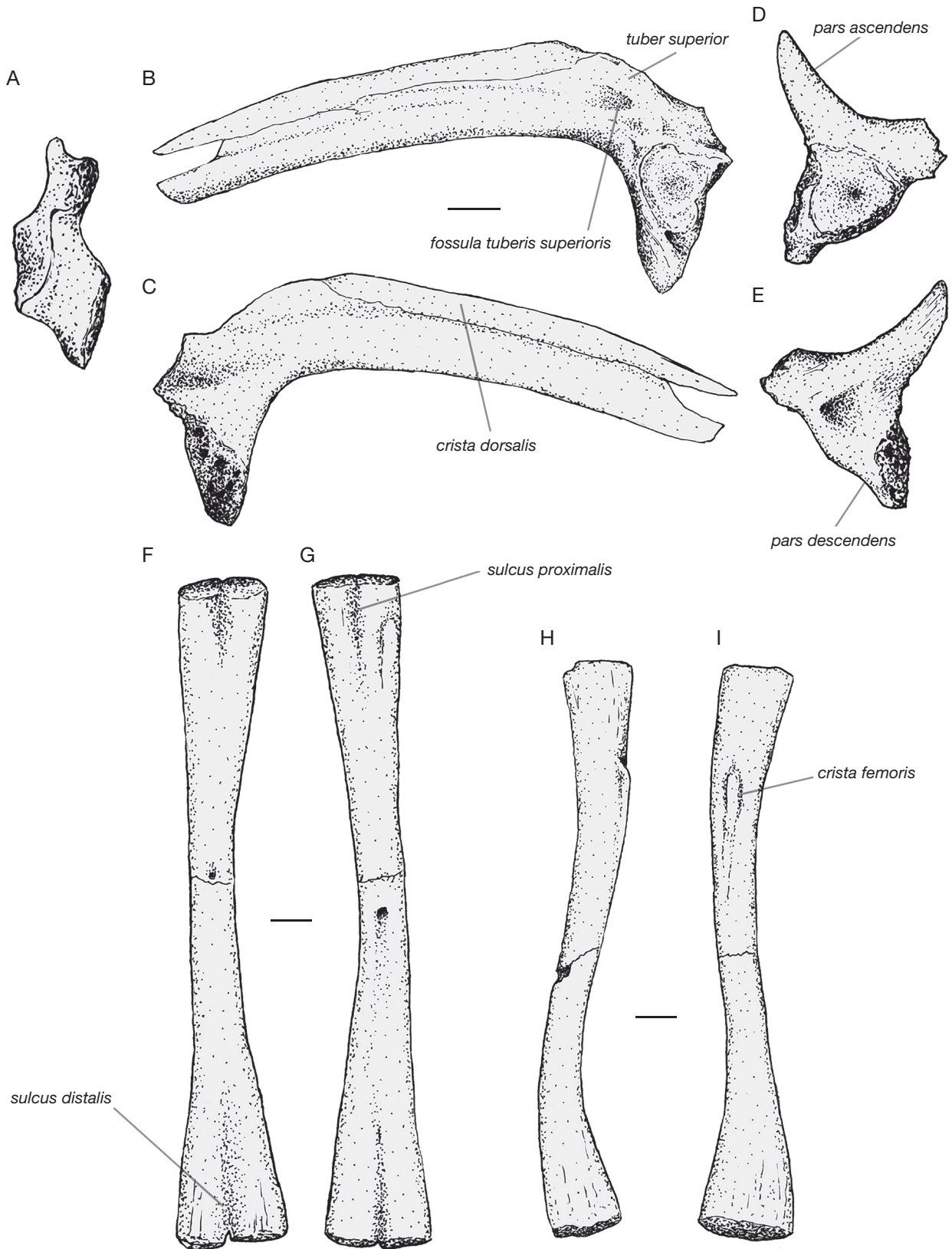
FIG. 8. — *Latonia* sp.: **A-C**, left ilium (PFHER00005A) in symphyseal (**A**), lateral (**B**), and medial (**C**) views; **D, E**, right ilium (PFHER00005B) in lateral (**D**) and medial (**E**) views; **F, G**, left tibiofibula (PFHER00041A) in ventral (**F**) and dorsal (**G**) views; **H, I**, right femur (PFHER00038B) in ventral (**H**) and dorsal (**I**) views. Scale bars: 3 mm.
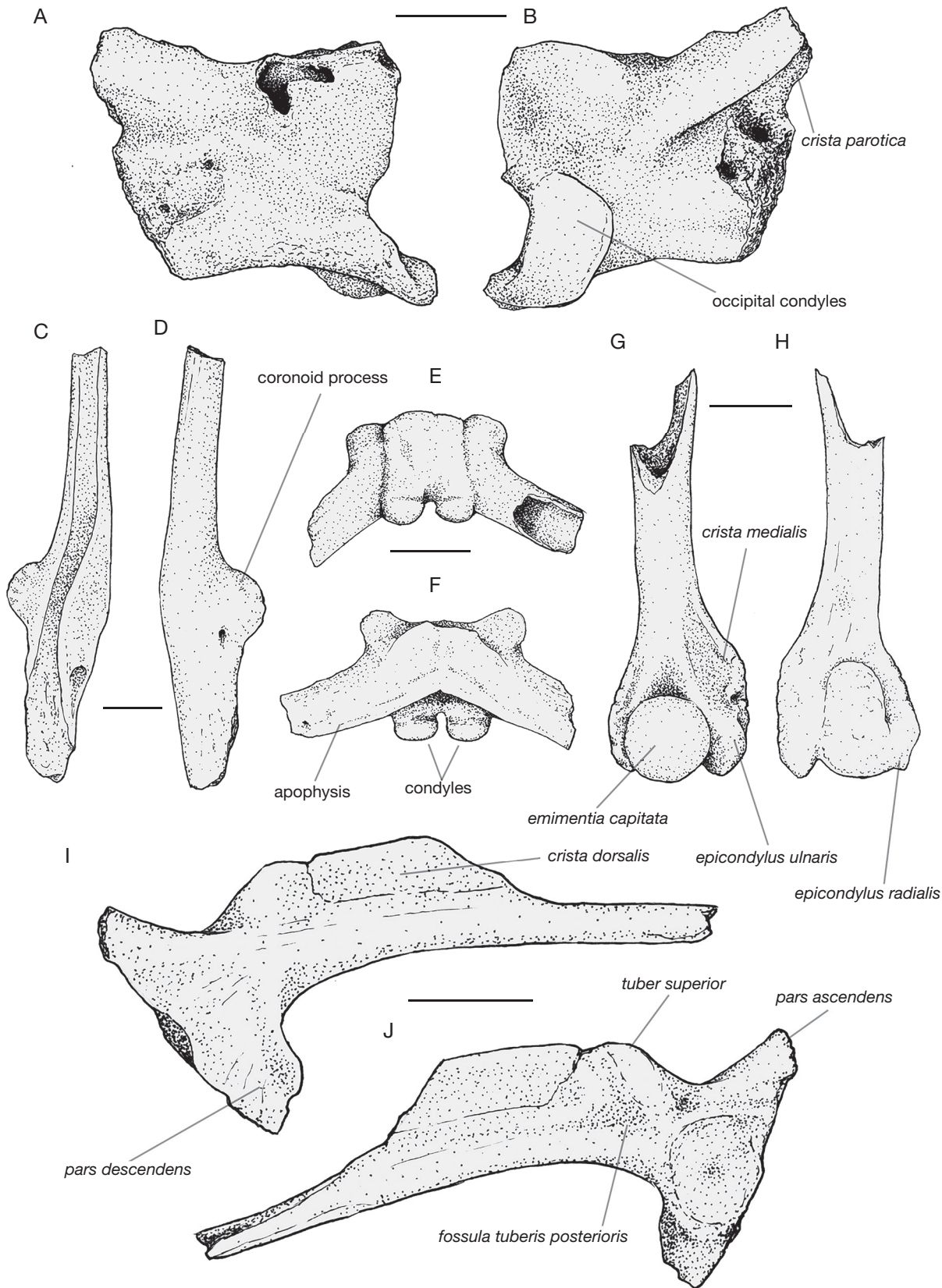
FIG. 9. — *Pelophylax* sp.: **A**, **B**, right prootico-occipital (PFHERP00052) in anterior (**A**) and posterior (**B**) views; **C**, **D**, right prearticular (PFHERP00057) in dorsal (**C**) and ventral (**D**) views; **E**, **F**, sacral vertebra (PFHERP00053) in ventral (**E**) and dorsal (**F**) views; **G**, **H**, right humerus (PFHERP00062) in ventral (**G**) and dorsal (**H**) views; **I**, **J**, left ilium (PFHERP00064) in medial (**I**) and lateral (**J**) views. Scale bars: 3 mm.

This feature is absent in both *L. seyfriedi* (or *L. gigantea*, see above; Villa *et al.* 2019) and *L. nigriventer* (Biton *et al.* 2016), but the lack of described pterygoids attributed to the other species hinders a comparison with them. Moreover, the *prominentia ducti semicircularis posterioris* of the prootico-occipital also shows a peculiar morphology: despite being present in all *Latonia* species (unknown in *L. vertaizoni*), the one visible on the Pietrafitta specimens is very long (longer than in *L. ragei*, and some specimens of *L. caucasica* and *L. seyfriedi*) and displays a ventral extension that reaches the occipital condyle, unlike any other *Latonia* species for which the prootico-occipital is described, in which the extension is either absent or terminating far from the condyle (Roček 1994; Syromyatnikova & Roček 2019).

Taking all the above-mentioned features into consideration, it is difficult to clearly identify the *Latonia* from Pietrafitta at the species level and, due to the peculiar morphological characters it displays, it may be possible that it represents a new species. However, more detailed comparisons and a revision of the genus *Latonia* would be necessary to refer the material from Pietrafitta to a species within *Latonia*. Hence, we assign it to *Latonia* sp.

Family Ranidae Rafinesque-Schmaltz, 1818
Genus *Pelophylax* Fitzinger, 1843

Pelophylax sp.
(Fig. 9)

Referred material. — PFHERP00074, PFHERP00090, PF-HERP000100: 3 maxillae; PFHERP00052A, PFHERP00052B: 2 prootico-occipitals; PFHERP00049, PFHERP00057, PF-HERP000101: 9 prearticulars; PFHERP00095: 3 thoracic vertebrae; PFHERP00053: 1 sacral vertebra; PFHERP00059, PFHERP00099: 2 urostyles; PFHERP00066: 1 scapula; PFHERP00054, PF-HERP00065: 2 coracoids; PFHERP00062, PFHERP00072, PF-HERP00077, PFHERP00081, PFHE3RP00082, PFHERP00091, PFHERP000102: 17 humeri; PFHERP00060, PFHERP00076: 7 radioulnae; PFHERP00048, PFHERP00064, FHERP00078, FHERP00085: 13 ilia; PFHERP00051, FHERP00086: 4 ischia; PFHERP00071, PFHERP00088, PFHERP00092, PFHERP00098: 7 femora; PFHERP00055, PFHERP00061, PFHERP00079, PF-HERP00083, PFHERP00089, PFHERP00069, PFHERP00094: 8 tibiofibulae; PFHERP00050, PFHERP00068, PFHERP00069, FHERP00087, FHERP00093: 12 tarsals; PFHERP00070: 3 phalanges; PF-HERP00056, PFHERP00058, PFHERP00063, PFHERP00067, PFHERP00073, PFHERP00096: 13 indeterminate elements (Fig. 9).

Description
The remains referred to *Pelophylax* sp. here include maxillae with pedicellate, pleurodont, and densely-packed teeth, a smooth lateral surface, and a well-developed *lamina horizontalis*, which is placed medially. None of them preserves the *processus palatinus*. The prootico-occipitals (Fig. 9A, B) are poorly preserved, but they have a half-moon shaped condyle, which is surmounted by a small bump. All prearticulars (Fig. 9C, D) solely preserve the coronoid process, which is quite high and laterally characterized by a series of shallow furrows and ridges. In all specimens, a foramen is present on the

lateral side of this bone. The sacral vertebra (Fig. 9E, F) has an anterior condyle and shows two posterior condyles for the articulation with the urostyle. The two transverse apophyses are cylindrical and slightly inclined posteriorly. The neural arch is small and bears a low keel that extends laterally along the dorsal surfaces of the transverse apophyses. Only one of the two urostyles (PFHERP00059) is complete. The *crista dorsalis* is quite high and shows no sign of dorsal fissures. There are two subrounded anterior cotyles for the articulation with the sacral vertebra and no transverse processes. In the coracoids, the *pars glenoidalis* is large and flattened, whereas the pars epicoracoidealis is almost laminar and has a fan-shaped outline. The main body is strongly constricted in the middle portion, with a concave anterior margin and an almost rectilinear posterior margin. All of the humeri (Fig. 9G, H) lack the proximal half of the bone. The robust diaphysis is quite straight in its preserved portion. The *eminentia capitata* is rounded and is a natural extension of the shaft. In the best-preserved specimen (PFHERP00062), a part of the *crista ventralis* is preserved, whereas there are no signs of *crista paraventralis*. The *epicondylus ulnaris* is quite distinct and reaches the distal margin of the *eminentia*. On the contrary, the *epicondylus radialis* is weakly developed. The medial crest, which is not deflected dorsally, is relatively short proximodistally, but protrudes relatively far laterally. In some specimens, it displays rugosities on the ventral side. In other specimens, the medial crest can be strongly reduced. This different development is commonly attributed to sexual dimorphism (see e.g. Bailon 1999), possibly related to larger forelimb muscles related to amplexus (and consequently more developed crests) in male frogs (Navas & James 2007; Mao *et al.* 2014). In most of the specimens, the medial crest is less developed compared to the lateral one. The radioulnae are elongated, but slender. The ilia (Fig. 9I, J) have a high and prominent *crista dorsalis* and a well-developed *tuber superior*. The *pars ascendens* is short. The *tuber superior* and *pars ascendens* are roughly perpendicular to each other. The ilia show a deep supracetabular fossa, either an extremely shallow or no preacetabular fossa, and no interiliac groove. The strong development of the *tuber superior* marks a wide *fossula tuberis superioris* on the lateral surface of the *crista dorsalis*. The femora are sigmoidal, with no *crista femoris*. The tibiofibulae are long and slender, with a concave lateral margin. At both epiphyses, the tibial and fibular components of these bones are elliptical; the main axes of these ellipses are convergent in proximal and distal views. Other elements, such as the fragmented scapula and several parts of the tarsals, cannot be described due to the poor preservation.

Remarks
The fossils of a small anuran unearthed from Pietrafitta are clearly different from the ones belonging to the large-sized *Latonia*. In particular, humeri and ilia are very useful for the identification. The combination of humeral features like the straight and robust shaft with the *eminentia* located on the same axis of the diaphysis, the absence of *crista paraventralis*, and the not-deflected medial crest are typical of the group

of green frogs, genus *Pelophylax* (Bailon 1999). This genus is also distinguishable from the quite similar *Rana*, the brown frogs, for the morphology of the ilia. The well-developed *crista dorsalis*, the well-defined *tuber superior*, and the angle of 90° between the tuber and the anterior border of the *pars ascendens* is a combination of features that is diagnostic of *Pelophylax* (Bailon 1999). The lack of a complete skeleton from Pietrafitta and the general difficulty in recognizing *Pelophylax* species based on osteological characters (Blain *et al.* 2015) do not allow us to infer more about the identification of these anuran remains.

Class REPTILIA McCartney, 1802
Order TESTUDINES Batsch, 1788
Family EMYDIDAE Bell, 1825
Genus *Emys* Duméril, 1805

Emys gr. *orbicularis* Linnaeus, 1758
(Figs 10; 11)

REFERRED MATERIAL. — PFAHER00105: 1 fragmentary costal, 1 fragmentary peripheral, 2 hyoplastra (R and L), 2 hypoplastra (R and L), 2 xiphiplastra (R and L), 8 plastron fragments, 9 shell fragments; PFAHER00106: 1 nuchal, 1 complete neural series (8 neurals), suprapygal, pygal, 6 fragmentary right costals (II, IV to VIII), 8 fragmentary left costals (I to VIII), 2 right peripherals (X, XI), 11 left peripherals (I to XI), 1 entoplastron, 2 hyoplastra (R and L), 1 hypoplastron (L), 2 xiphiplastra (R and L), 58 shell fragments, 2 humeri (R and L), 2 femora (R and L), 1 fragmentary scapula, 1 fragmentary acromion, 2 ilia (R and L), 7 fragmentary cervical vertebrae, 6 vertebral fragments, 6 caudal vertebrae, 1 terminal phalanx; PFAHER00107: 2 hypoplastra (R and L), 1 xiphiplastron (R), 5 plastron fragments; PFAHER00108: fragments of two specimens - first specimen: 16 costal fragments; 7 peripheral fragments (two of which from the bridge); 2 epiplastra (R and L), 1 fragmentary entoplastron, 1 hyoplastron (L), 2 hypoplastra (R and L), 11 plastron fragments, 26 shell fragments; second specimen: 1 bridge peripheral; 1 epiplastron (R), 3 shell fragments; PFAHER00109: fragments of two specimens - first specimen: 1 fragmentary nuchal, 1 neural, 2 fragmentary costals, 2 peripherals, 1 fragmentary epiplastron (L), 1 fragmentary entoplastron, 1 fragmentary hyoplastron (R); 1 fragmentary xiphiplastron ? (R), 42 shell fragments; second specimen: 1 epiplastron (L); PFAHER00110: 1 nuchal, 6 neurals, 3 costals (IR, IL, IIL), 22 fragments of costals, 6 peripherals (IR, IIR, I to IVL), 12 peripherals indet., 1 pygal, 1 nearly complete plastron (L hypoplastron and xiphiplastron missing), 22 shell fragments, 1? fragmentary vertebra; PFAHERP00111: fragments of two specimens - first specimen: 3 cervical vertebrae, 2 caudal vertebrae, 2 humeri (1R, 1L), 1 scapula-acromion (L), 1 coracoid (L?), 2 acromions (R and L), 1 ulna, 1 ilium (R); second specimen: 1 humerus (L); PFAHERP00112: 1 coracoid, 1 terminal phalanx; PFAHERP00113: 1 hyoplastron (R), 1 hypo- and xiphiplastron fused (L), 3 shell fragments, 1 fragmentary dentary (L), 1 fragmentary coracoid, 1 fragmentary ulna, 1 fragmentary ? radius, 6 metapodials, 1 fragmentary vertebra; PFHER00114: partial plastral anterior lobe; PFHER00115: partial plastron; PFHER00117: partial plastral posterior lobe; PFHER00118: carapace; PFHER00119: slightly incomplete plastron; PFHER00120: partial plastron; PFHER00121: partial plastral posterior lobe; PFHER00122: ?hyoplastron; PFHER00123: entoplastron; PFHER00124: partial plastral posterior lobe; PFHER00125: 1 epiplastron (R), 1 epiplastron (L), fragmentary hypoplastron (R), fragmentary xiphiplastron (R); PFHER00126: 2 fragmentary ? hypoplastra (R and L), 1 xiphiplastron (L); PF-

HER00127: very fragmentary plastron (L epiplastron, L hyoplastron, L hypoplastron, L xiphiplastron, R xiphiplastron); PFHER00128: posterior lobe; PFHER00129: nearly complete plastron (only R hypoplastron missing); PFHER00130: 2 xiphiplastra (R and L), 1 fragmentary hypoplastron (R), 1 plastral fragment; PFHER00131: partial shell; PFHER00132: nearly complete carapace; PFHER00133: partial shell; PFHER00134: partial carapace; PFHER00135: nearly complete shell (Figs 10; 11).

DESCRIPTION

The abundant fossils from Pietrafitta allow us to provide a general description of the whole shell. It is characterized by the absence of a firm sutural connection of the carapace and the plastron (replaced by a ligamental connection involving the peripherals of the bridge – from IV to VII) and by the presence of a hinge between the hyo- and hypoplastra. The cervical scute is narrow (longer than broad) and shorter than one third of the anteroposterior length of the nuchal. The neural formula is 4-6A-6A-6A-6A-6A-6A-6A(?). Apparently, there is only one suprapygal (not crossed by any sulcus). The first vertebral does not cover the nuchal completely and the marginals do not cover the peripherals completely (just for about half of their external surface). The pygal element hosts therefore both the intermarginal and the vertebromarginal sulci. The costals are rather rectangular (not markedly trapezoidal) and, if separated from the peripherals, show a well-developed distal process that enters a hole in the corresponding peripheral. On the visceral surface of the costals, the proximal end of the rib is anteroposteriorly broad and straight. The epiplastral pads are weakly developed and anteroposteriorly very thin along the midline. The gulars enter the entoplastron that is grazed (or very marginally crossed) by the humeropectoral sulcus. The pectoroabdominal sulcus is rather straight and located nearly at the hyohypoplastral hinge. The abdominofemoral sulcus is anteriorly concave (see PFHERP135 in Fig. 10C and PFHERP00115 in Fig. 11F). The weakly sigmoid femoroanal sulcus terminates medially very far from the hypoxiphiplastral suture; it might correspond to a weak concavity at the lateral edge of the xiphiplastra. The dorsal fold of the humeral shield on the epiplastron and hyoplastron as well as that of the femoral shield on the hypoplastron and the xiphiplastron are very broad. The anal notch is variably developed, but it is generally broad (more than 90°) and moderately deep.

All the available acromions (specimens: PFAHER00106, PFAHERP00111) are characterized by a marked dorsal longitudinal ridge (Fig. 11B, G).

REMARKS

The identification of the fossil material listed and described here, including complete or nearly complete shells, does not pose any problem due to its overall congruence with extant *Emys orbicularis*, despite the presence of some peculiarities. All the characters listed in the section above fit well with the diagnostic features discussed by Holman (1995), Hervet (2000), and Fritz *et al.* (2011) for *E. orbicularis*. The only peculiar features in the Pietrafitta material are related to the acromion and the plastron. The occurrence of a marked
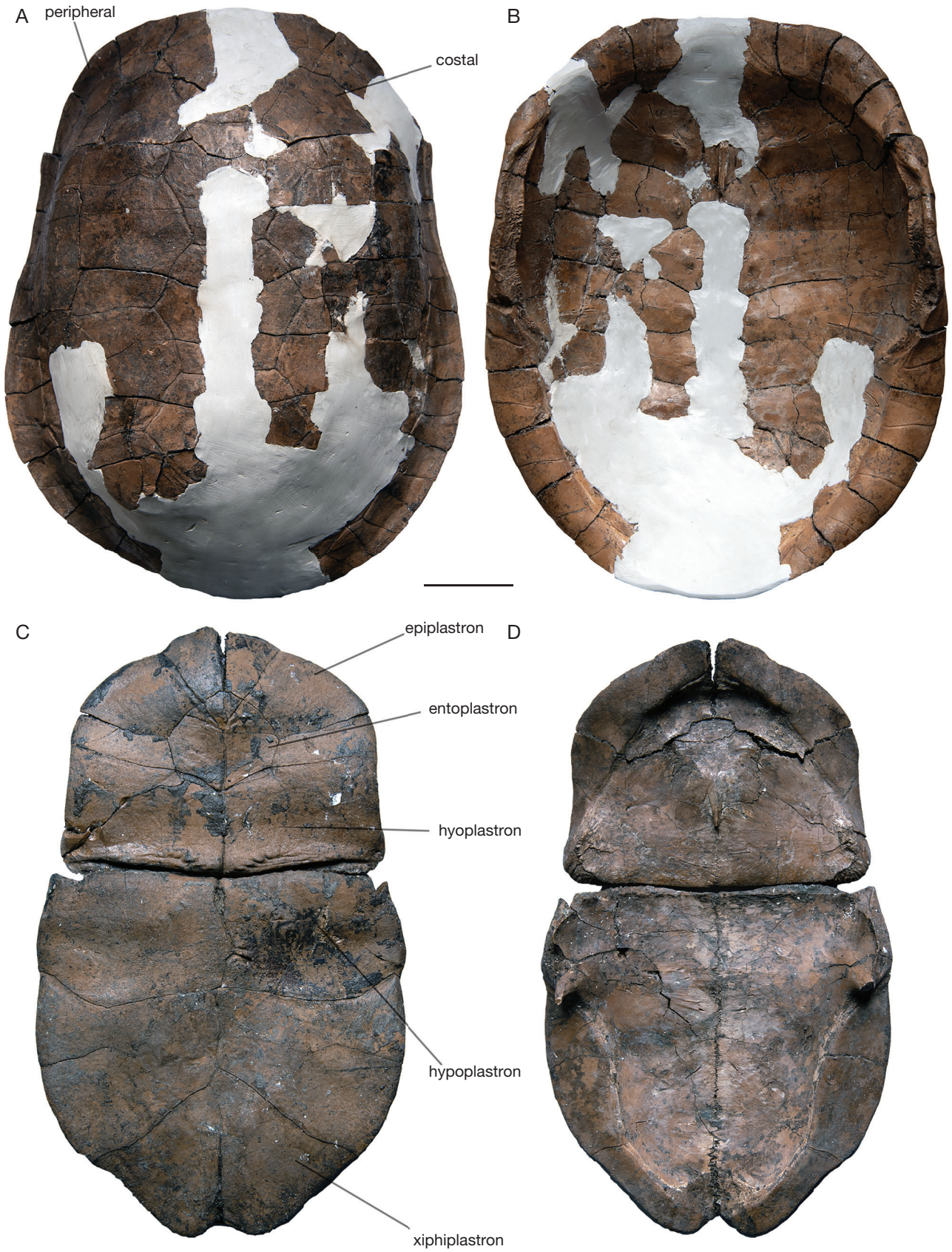
FIG. 10. — *Emys* gr. *orbicularis* Linnaeus, 1758: nearly complete shell (PFHERP135): **A**, **B**, carapace in external (**A**) and visceral (**B**) views; **C**, **D**, plastron in external (**C**) and visceral (**D**) views. Scale bars: 3 cm.
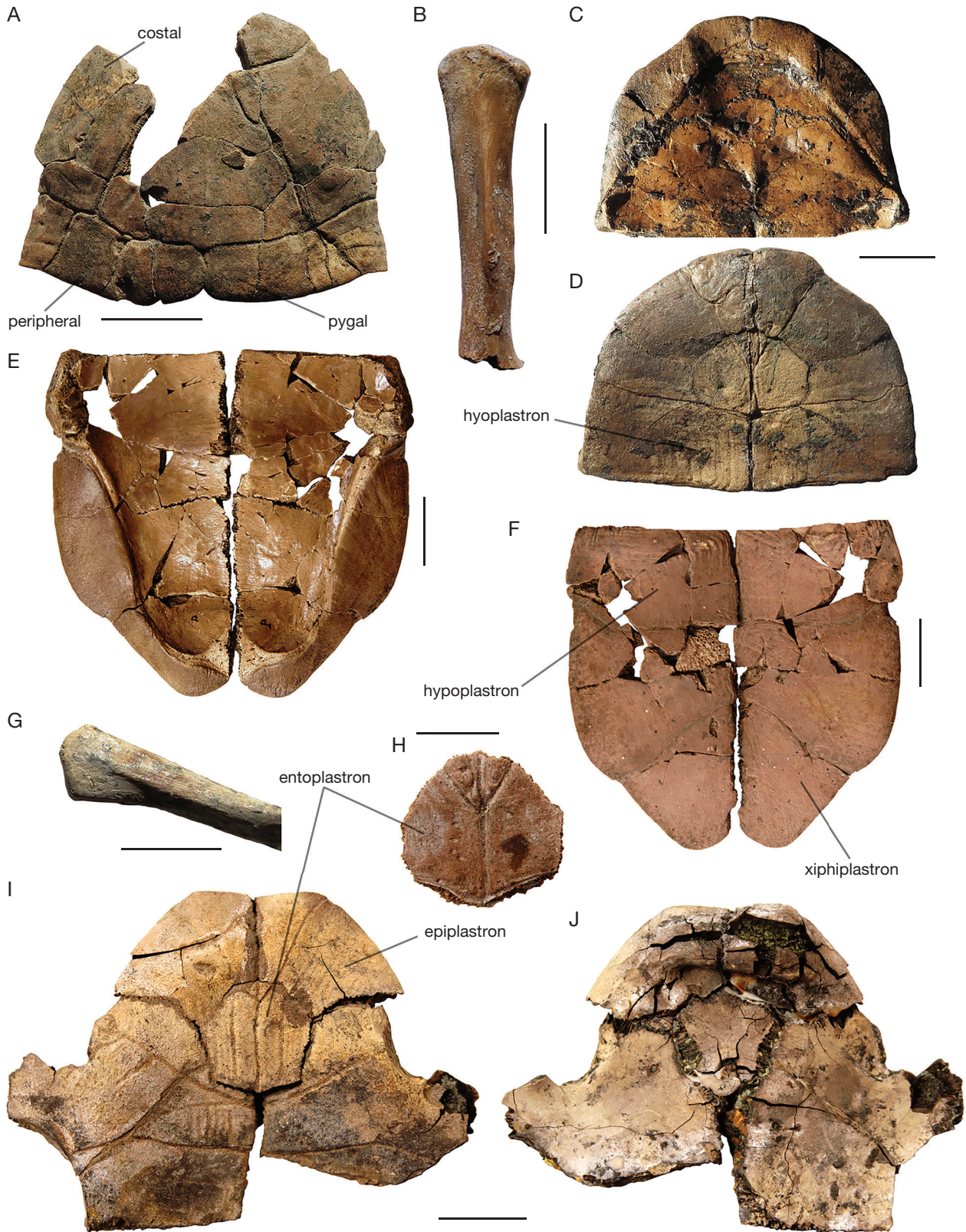
Fig. 11. — *Emys* gr. *orbicularis* Linnaeus, 1758: **A**, posterior shell portion (PFHERP131) in posterior view; **B**, acromion (PFHERP00112) in dorsal view; **C**, **D**, plastral anterior lobe (PFHERP00106) in dorsal (**C**) and ventral (**D**) views; **E**, **F**, plastral posterior lobe (PFHERP00115) in dorsal (**E**) and ventral (**F**) views; **G**, acromion (PF-HERP00111) in dorsal view; **H**, entoplastron (PFHER00123) in ventral view. *Testudo hermanni* Gmelin, 1789: **I**, **J**, plastral anterior lobe (PFHER00116) in ventral (**I**) and dorsal (**J**) views. Scale bars: 3 cm.

longitudinal ridge on the acromions (Fig. 10B, G) has not been reported in the literature and is also absent in the extant *Emys* specimens that we checked for this character (*Emys orbicularis* MDHC 43 – juvenile, 430, and 468-470; NNHC-HUJ-Z-223, 246, and 346; *Emys trinacris* Fritz *et al.*, 2005 MDHC 200, 471). However, it is possible that we simply do not have enough specimens available to grasp the entire morphological variability within the species of *Emys*. The morphology of the plastron is characterized by an anteriorly concave abdominofemoral sulcus (somehow reminiscent of that of the poorly known extinct species *Emys wermuthi* Młynarski, 1956), and by markedly expanded dorsal folds of the humeral and femoral shields that are not so developed in our comparative material of *E. orbicularis* (as well as in the literature). The variability of all these characters in *E. orbicularis* should be further investigated. Because it is possible that extant *E. orbicularis* is indeed a complex of species (Fritz *et al.* 2011), and because the recently recognized extant species *Emys trinacris* (Fritz *et al.* 2005) has a shell that is morphologically identical to that of *E. orbicularis*, we only refer the material from Pietrafitta to *Emys* gr. *orbicularis*, i.e., a group including both taxa. Nevertheless, the fact that *E. trinacris* is an endemic Sicilian species renders its past presence in peninsular Italy unlikely.

The presence of *E. orbicularis* at Pietrafitta is known since Ambrosetti *et al.* (1977), but the fossil material was first described by Kotsakis & Gregori (1985: 1) based on uncatalogued, "un certo numero di resti di carapaci e piastroni" [a certain number of remains of carapaces and plastra], limb bones, and girdle elements. According to our analysis none of the elements currently available in the Pietrafitta vertebrate collection correspond to those figured by Kotsakis & Gregori (1985).

Family TESTUDINIDAE Gray, 1825
Genus *Testudo* Linnaeus, 1758

Testudo hermanni Gmelin, 1789
(Fig. 11)

REFERRED MATERIAL. — PFHER00116: 1 plastral anterior lobe (Fig. 11I, J).

DESCRIPTION
The anterior plastral lobe PFHER00116 is only partially preserved due to the incompleteness of the left hyoplastron. Moreover, the epiplastral pads are partly crushed. However, it is clear that the anterior edge of the lobe is broad and truncated. The entoplastron is triangular in visceral view and slightly longer than broad. The hyoplastron was sutured to the corresponding marginal elements of the carapace, as shown by the few remnants of the lateral sutural surfaces and by the well-developed plastral buttresses. Growth marks are visible on the left epiplastron, the entoplastron, and the right hyoplastron. The gulars occupy the medial third of the external surface and slightly enter the entoplastron posteriorly.

The humeropectoral sulcus is broadly concave medially and does not enter, not even grazes, the entoplastron. The pectoroabdominal sulcus is moderately convex. On the visceral surface, the partly crushed epiplastral pads are only modestly thick and slightly overhanging posteriorly (they do not overhang the entoplastron in dorsal view) without developing a significant gular pocket. The visceral surface of the entoplastron is longer than broad.

REMARKS
Several characters of specimen PFHER00116 allow referral to *Testudo hermanni*. Among others, these are the moderately thick epiplastral pads that do not define a gular pocket and the visceral surface of the entoplastron that is longer than wide and rather triangular (see characters in Amiranashvili 2000 and Hervet 2000). The position of the humeropectoral sulcus, which does not enter or even graze the entoplastron, is commonly present in the western subspecies *Testudo hermanni hermanni* (Lapparent de Broin *et al.* 2006), which inhabits peninsular Italy since at least the Early Pleistocene (Rook *et al.* 2013; TTWG 2017).

Order SERPENTES Linnaeus, 1758
Family COLUBRIDAE Oppel, 1811
Taxon "Colubrines" *sensu* Szyndlar (1984)

"Colubrines" indet.
(Fig. 12)

REFERRED MATERIAL. — PFHERP00080: 1 precloacal vertebra (Fig. 12A-E).

DESCRIPTION
The vertebra (Fig. 12A-E) is heavily damaged, but it still preserves part of the prezygapophyseal processes, the zygosphene, and the postzygapophyses. The neural spine is missing at the base. The ventral surface of the centrum is damaged, but a hint of either a broken hypapophysis or at least a small keel seems to be present on the ventral side. The cotyle and condyle are depressed. The neural arch is dome shaped in posterior view. Two distinct paracotylar foramina are present in the two depressions lateral to the cotyle. The dorsal margin of the zygosphene is convex (characterized by two lateral lobes and a small medial one) its anterior margin is vaulted, arching dorsally.

REMARKS
The small vertebra PFHERP00080 is heavily damaged, but a vaulted arch on the posterior portion of the bone is recognizable. A broken surface is visible on the ventral side, so the presence of a broken hypapophysis cannot be excluded, but the extremely flat ventral surface rather suggests the presence of a keel than a hypapophysis. This morphology allows us to refer this fossil to a snake belonging to the operative taxon "Colubrines" (Szyndlar 1984, 1991a), but its preservation status hinders further comments.
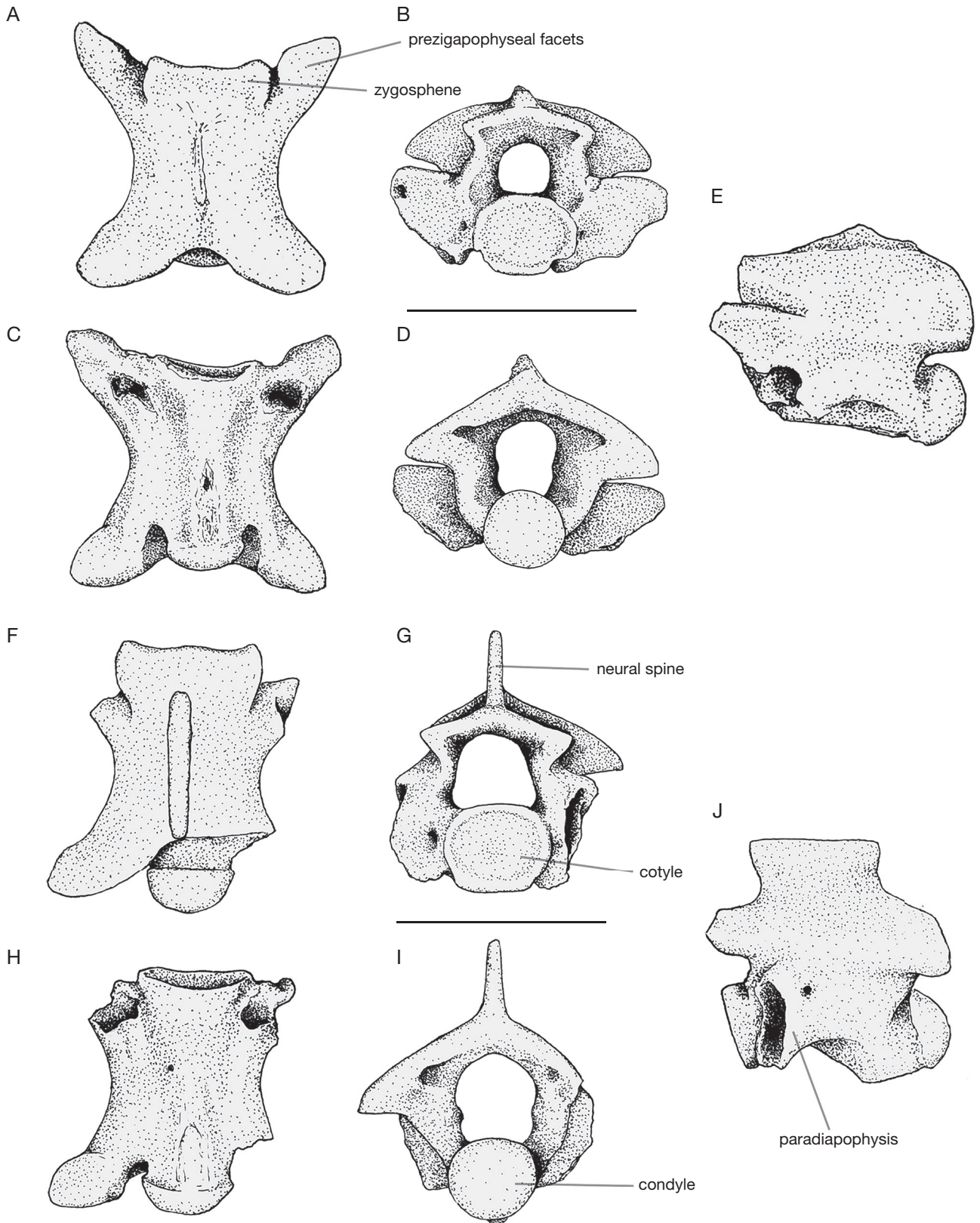
Fig. 12. — "Colubrines" indet.: **A-E**, presacral vertebra (PFHERP00080) in dorsal (**A**), anterior (**B**), ventral (**C**), posterior (**D**), and left lateral (**E**) views. *Natrix* sp.: **F-J**, presacral vertebra (PFHERP00084) in dorsal (**F**), anterior (**G**), ventral (**H**), posterior (**I**), and left lateral (**J**) views. Scale bars: 3 mm.

Subfamily NATRICINAE Bonaparte, 1838
Genus *Natrix* Laurenti, 1768

Natrix sp.
(Fig. 12)

REFERRED MATERIAL. — PFHERP00084: 1 precloacal vertebra (Fig. 12F-J).

DESCRIPTION

The single vertebra (Fig. 12F-J) is partly preserved. It misses most of the hypapophysis, paradiapophyses, prezygapophyseal processes, both parapophyseal processes, and the right postzygapophyseal articular facet. The vertebra is quite small and has a relatively short and narrow centrum with dorsoventrally depressed cotyle and condyle. The broken hypapophysis is completely missing, even if a well-developed anterior keel is still present. The left postzygapophyseal facet is ovoidal and inclined posteroventrally. Posteriorly, the neural arch is high and vault-shaped. The subcentral ridges are well marked. Only the right large paracotylar foramen is still distinguishable, located in a depression lateral to the cotyle. The lateral foramina are small but distinct and situated in shallow depressions beneath the interzygapophyseal ridges. The zygosphene is slightly convex dorsally and shows three distinct lobes (one median and two lateral), whereas, anteriorly, the margin is dorsally arched. The neural spine is high and slightly inclined caudally.

REMARKS

The single precloacal vertebra PFHERP00084 is characterized by its small size, light built, vaulted posterior neural arch, and relatively high neural spine. On the ventral side, a broken irregular surface is clearly visible, which implies the original presence of a hypapophysis. These features allow us to assign this vertebra to the subfamily Natricinae and, in particular, to the genus *Natrix*, which is characterized by a lightly built morphology and high neural spines (Szyndlar 1984, 1991b). Due to the bad preservation of the fossil, no further assumptions about the specific attribution of this fossil can be made.

Family VIPERIDAE Laurenti, 1768
Subfamily VIPERINAE Laurenti, 1768
Genus *Vipera* Laurenti, 1768

Vipera (*s.l.*) sp. (cf. gr. "Oriental vipers")
(Fig. 13)

REFERRED MATERIAL. — PFHER00104: 1 precloacal vertebra (Fig. 13).

DESCRIPTION

The single precloacal vertebra (Fig. 13) is relatively large (centrum length: 6.6 mm). The neural spine, the zygosphene, and the prezygapophyseal processes are missing, whereas paradiapophyses, postzygapophyses, and the hypapophysis are preserved, even though slightly damaged. The vertebra has a large and relatively short centrum, with a very broad cotyle and a robust condyle, both of which are slightly depressed dorsoventrally. The hypapophysis is long and straight, and projects posteroventrally. The prezygapophyseal facets are elliptical, whereas the postzygapophyseal articular facets are more circular. Both are slightly inclined dorsally. The prezygapophyseal processes are quite short and pointed. The synapophysis is clearly divided in the dorsal diapophysis and, below, the ventral parapophysis, which is separated from the cotyle by a small and shallow groove. Part of the parapophyseal process is missing. The short neural arch is relatively depressed and has an almost rectilinear dorsal margin in caudal view. Paracotylar, subcentral, and lateral foramina are medium sized. The paracotylar foramina are located in distinct depressions. The neural spine is broken at the base and therefore it is impossible to assess its shape or height.

REMARKS

PFHER00104 can be referred to the genus *Vipera* (*s.l.*) based on the presence of the following combination of features (Szyndlar 1984, 1991b): a long and straight hypapophysis, dorsally inclined zygapophyseal articular facets, large cotyle and condyle, the dorsoventral compression of the neural arch, which also has an almost rectilinear posterodorsal margin in caudal view. The large size and the craniocaudal compression of the vertebra allow us to exclude a referral of the Pietrafitta viper to the *Vipera berus* Linnaeus, 1758 complex (Szyndlar 1991b). It is equally possible to exclude *Daboia* due to the extremely large size reached by the snakes belonging to this latter genus. These observations restrict the possible referral of PFHER00104 to two groups: the *Vipera aspis* Linnaeus, 1758 complex or the "Oriental vipers" complex. The size and robustness of the vertebra allows an attribution to a medium-sized "Oriental viper", the vertebral morphology of which is very reminiscent of the Pietrafitta specimen. The *V. aspis* complex includes small- to medium-sized vipers from Europe. All the species belonging to this complex have a smaller size compared to the specimen recovered from Pietrafitta except for the largest species, *Vipera ammodytes* Linnaeus, 1758. The morphology of all the "Oriental vipers" and *V. ammodytes* is quite similar, thus it is not easy to recognize the different species from single incomplete vertebrae. One of the few diagnostic features that are used to distinguish these snakes is the size of the neural spine, but this structure is missing in the Pietrafitta vertebra.

To support identification, measures of PFHER00104 were compared with those of different fossils and modern vertebral elements of *V. ammodytes* (to which PFHER00104 was referred in a previous preliminary account; Delfino 2002), as well as "Oriental vipers" following the methodology of Codrea *et al.* (2017) (Fig. 14). Our specimen shows close similarities in terms of size and general proportions with a very old and large *V. ammodytes* individual. However, the ratio between centrum length and neural arch width (CL/NAW) is slightly smaller, more similar to that typical of the "Oriental vipers". As shown in Figure 14, in which this ratio is compared with the total length of the centrum, the Pietrafitta specimen is characterized by a long but wide
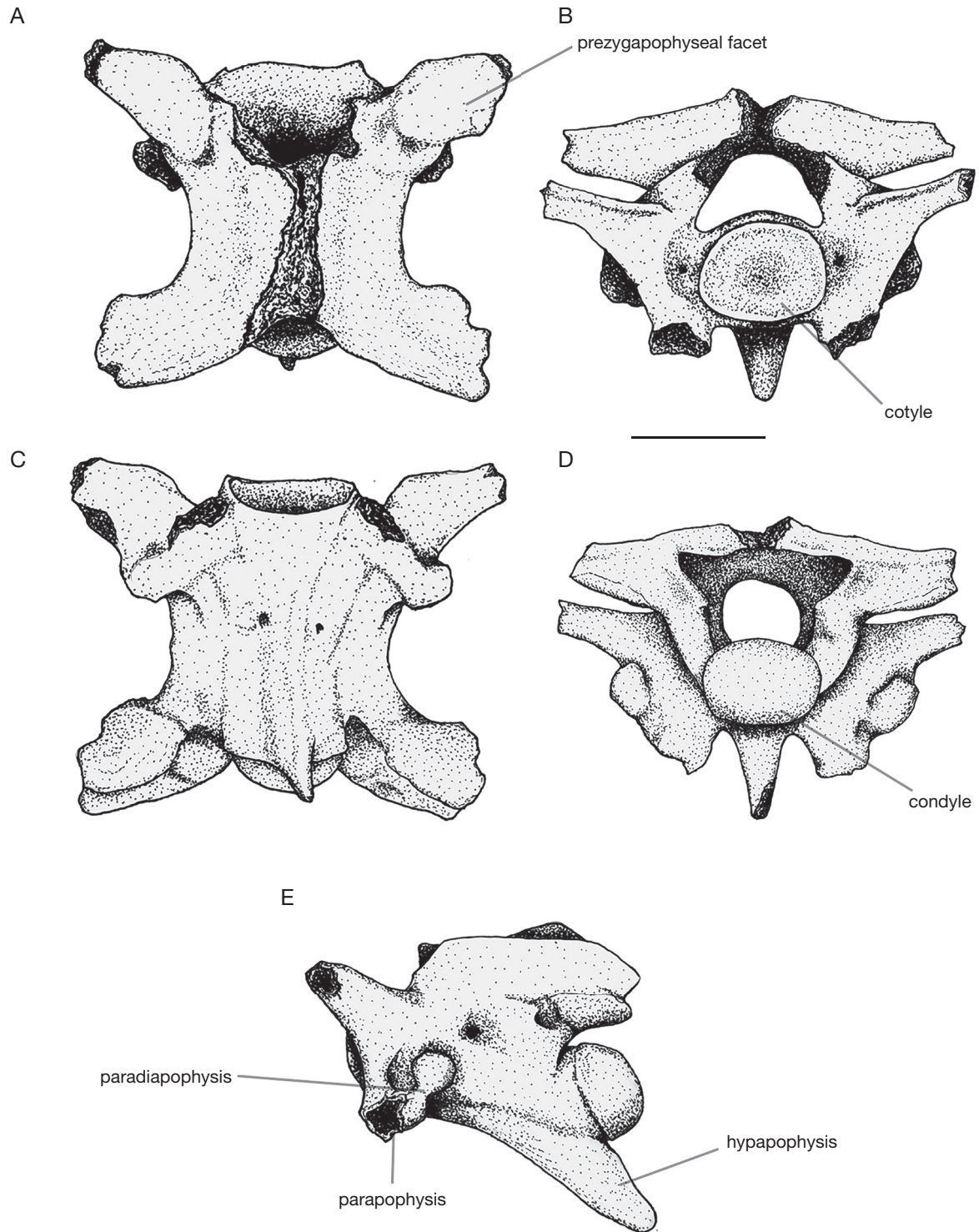
FIG. 13. — *Vipera* (*s.l.*) sp. (cf. gr. "Oriental vipers"): **A**-**E**, presacral vertebra (PFHER00104) in dorsal (**A**), anterior (**B**), ventral (**C**), posterior (**D**), and left lateral (**E**) views. Scale bars: 3 mm.
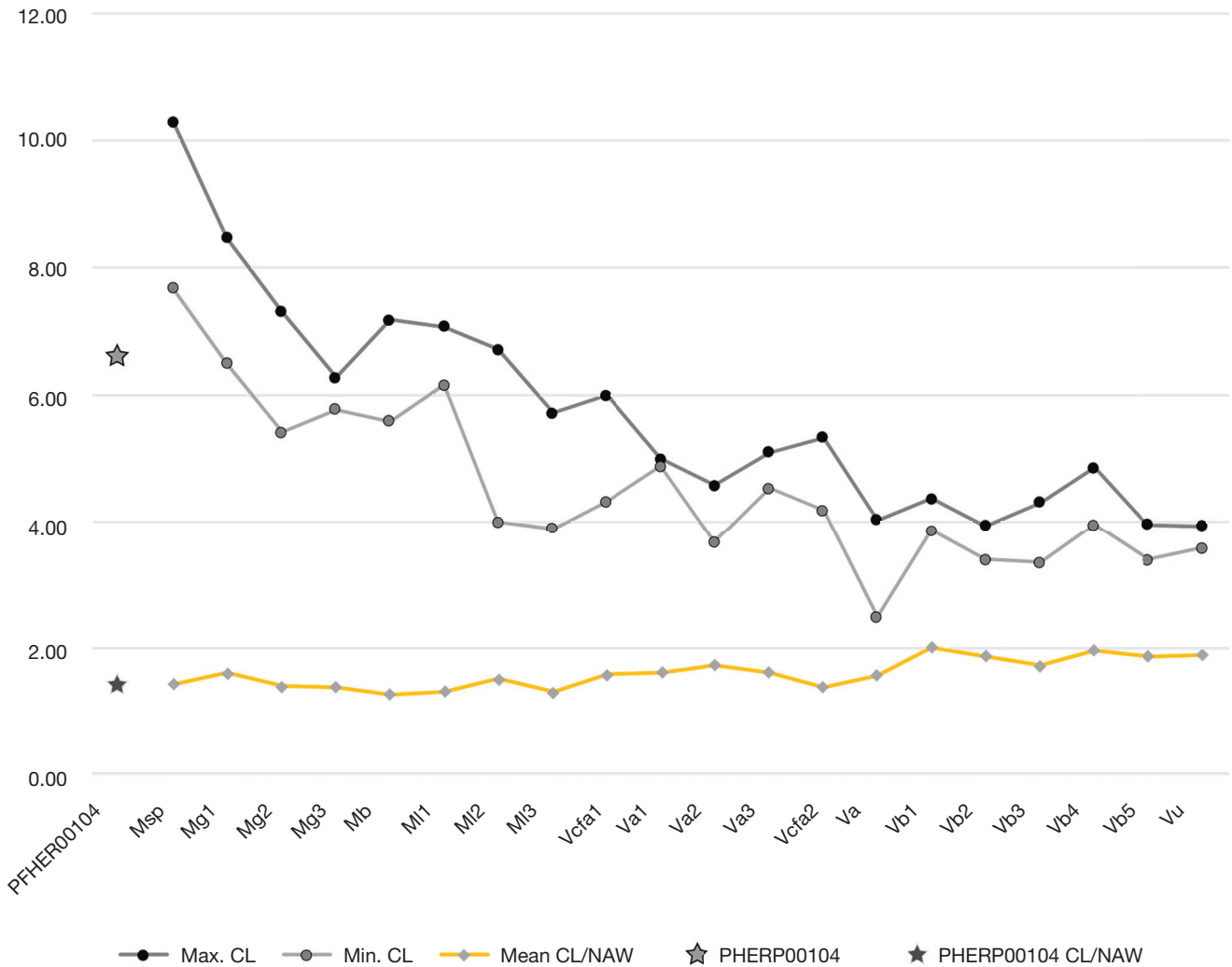
Fig. 14. — CL measurements of precloacal vertebrae and CL/NAW ratio in fossil and recent viperine snakes. Abbreviations: **Msp**, *Macrovipera* sp. Reuss, 1927 from Cretesti-1 (MN 9), Romania (N = 22) (Codrea *et al.* 2017); **Mg1**, *Macrovipera gedulyi* Bolkay, 1913 from Polgárdi 2 (MN 13), Hungary (N = 16) (Venczel 1994); **Mg2**, *Macrovipera gedulyi* from Polgárdi 4 "Upper" (MN 13), Hungary (N = 12) (Venczel 1994); **Mg3**, *Macrovipera gedulyi* from Polgárdi 4 "Lower" (MN 13), Hungary (N = 7) (Venczel 1994); **Mb**, *Macrovipera burgenlandica* Bachmayer and Szyndlar, 1987 from Kohfidisch (MN11), Austria (N = 11) (Bachmayer & Szyndlar 1987); **Ml1**, *Macrovipera lebetina* Linnaeus, 1758, recent (N = 25) (this paper); **Ml2**, *Macrovipera lebetina*, recent (N = 35) (this paper); **Ml3**, *Macrovipera lebetina*, recent (N = 15) (this paper); **Vcfa1**, *Vipera* cf. *ammodytes* Linnaeus, 1758 from Osztramos 1 (MN 14), Hungary (N = 10) (Venczel 2001); **Va1**, *Vipera ammodytes*, recent (N = 30) (Szyndlar 1984); **Va2**, *Vipera ammodytes* from Malà dohoda quarry (MQ1), Czech republic (N = 13) (Ivanov 1996); **Va3**, *Vipera ammodytes*, recent (N = 60) (Szyndlar 1991b); **Vcfa2**, *Vipera* cf. *ammodytes* from Betfia 12B (Lower Pleistocene), Romania (N = 8) (Venczel 2000); **Va**, *Vipera aspis* Linnaeus, 1758, recent (N = 25) (this paper); **Vb1**, *Vipera berus* Linnaeus, 1758 from Betfia 9 (Early Pleistocene), Romania (N = 16) (Venczel 2000); **Vb2**, *Vipera berus*, recent (N = 25) (Szyndlar 1991b); **Vb3**, *Vipera berus* from Mladec 2 (MQ2), Czech republic (N = 10) (Ivanov 2006); **Vb4**, *Vipera berus* from Malà dohoda quarry (MQ1), Czech republic (N = 20) (Ivanov 1996); **Vb5**, *Vipera berus*, recent (N = 25) (this paper); **Vu**, *Vipera ursinii* Bonaparte 1835, recent (N = 23) (this paper); **CL**, Centrum length; **NAW**, Neural arch width.

vertebra, with a ratio lower than 1.3. PFHER00104 has a wide centrum with stouter proportions compared to the analyzed *V. ammodytes* samples. Based on these results, we refer the specimen from Pietrafitta to the "Oriental vipers" complex, but with no further assumptions about the specific attribution. Moreover, we used the "cf." particle to highlight uncertainties due to the scarcity of fossil material.

DISCUSSION

The abundant ectothermic vertebrate remains from Pietrafitta considerably improve our knowledge of the local paleoenvi-

ronment as well as of the paleobiogeography of some relevant taxa correlated with the climate changes that affected the European continent during the Early Pleistocene.

The presence of several teleost taxa in the lignite deposits better defines the condition of the waterbodies present in the Pietrafitta basin during the considered time interval. The rudd (*Scardinius*) is a limnophilous teleost that inhabits nutrient-rich lakes, lowland rivers, backwaters, oxbows, and ponds with abundant submerged vegetation and muddy bottoms (Kottelat & Freyhof 2007). Rudds are typically phytophagous, but also feed on plankton and insects. The tench (*Tinca*) primarily inhabits lakes, ponds, and swampy areas, as well as slow moving rivers. In general, tenches prefer meso- and eutrophic

quiet waters with muddy bottom and a rich aquatic vegetation where they can feed on a variety of benthic organisms. Barbels are rheophilic teleosts that inhabit rivers and lakes where they prey on small actinopterygians and invertebrates, or feed on aquatic plants and algae (Kottelat & Freyhof 2007). These taxa confirm that a palustrine area with ponds and low energy rivers and, at least, a large permanent waterbody was present in the ancient Pietrafitta basin.

The interval between 1.8 and 1.2 Ma is characterized by a gradual "deterioration" of the climatic conditions in Europe. The tropical habitats typical of the Pliocene were replaced by temperate environments in most of the continental Europe, whereas in the Mediterranean areas (especially in the southernmost regions), there was an increase in aridity with the gradual disappearance of forested areas in favor of open landscapes. This cooling trend led to a floristic and faunal renewal on the entire continent, and several Pliocene taxa got extirpated or completely extinct (Kahlke *et al.* 2011). Most of the warm-climate faunal elements were replaced by new taxa that were better adapted to cooler environments and open landscapes. During the Villafranchian-Galerian transition, this replacement ultimately led to the so-called Early-Middle Pleistocene Transition (EMPT; Head & Gibbard 2005). These transitions affected not only the mammal faunas but also the herpetofauna of the continent with several groups of anurans and reptiles, previously mentioned, which faced extinction or a severe shrinkage of their distribution. The geography of Southern Europe, with several peninsulas wedged in the Mediterranean Sea, offered shelters for all the thermophilous taxa that were pushed South by the climate changes. Pietrafitta, located in the central part of the Italian Peninsula, could have been a suitable refuge for groups such as *Latonia* and the "Oriental vipers", which moved southward due to the progressive deterioration of the climatic conditions.

The first occurrence of *Latonia* dates back to the Oligocene. During the Miocene, due to the warm and humid climate, this genus rapidly colonized nearly the entire European continent (except for most of the islands and the northern regions) (Roček 1994). The Pliocene marked a decrease in the distribution of *Latonia*. The scanty fossil record indicates that the genus became restricted to the Mediterranean and eastern regions of Europe (Böhme & Ilg 2003; Ivanov 2007; Villa *et al.* 2019). These local extinctions were probably caused by deterioration of climatic conditions that eventually led to the extirpation of the genus in central and western Europe before the Middle Pleistocene (Szentesi 2019). On the contrary, the sister taxon of *Latonia*, *Discoglossus* Otth, 1837*,* expanded its range in all Europe during the Middle Pleistocene, showing its capability to adapt to these climatic changes (Roček 1994; Villa *et al.* 2019). Outside Europe, the most recent occurrence of the genus *Latonia* is in the Early Pleistocene of Turkey (Vasilyan *et al.* 2014) and this taxon is still represented by the extant population of *L. nigriventer* in northern Israel, which likely originated in the Pleistocene (Biton *et al.* 2013, 2016). In the Italian Peninsula, the last occurrences of *Latonia* have been reported from two localities: Arondelli (*Latonia* sp.; Pliocene, Triversa, Piedmont) and the Late Miocene-Early

Pliocene "Terre Rosse" of the Gargano Peninsula (*Latonia* cf. *L. gigantea* now *L. seyfriedi*) (Delfino 2002). Pietrafitta would be one of the southernmost European sites in which remains of this taxon have been found. Moreover, and probably more interestingly, this discovery represents, to date, the last occurrence of *Latonia* in Western Europe (see Szentesi 2019, for a Middle Pleistocene Latonia from Ungary).

Based on the morphology of the postcranial bones (e.g. possession of a moderately high *crista dorsalis* of the ilium), it is possible to consider the genus *Latonia* as particularly adapted jump and swim like the frogs belonging to the *Rana* Linnaeus, 1758 group ("brown frogs") (Böhme 2002; Tempfer 2005). It is likely that the reduction of the geographic distribution of *Latonia* during the Pliocene and the subsequent extinction in most of the European continent resulted in the concomitant occupation by other taxa of the niche left empty, such as *Rana* (Böhme 2002). Indeed, *Rana* does not occur in Miocene and Pliocene sites where *Latonia* is abundant (Böhme 2002; Tempfer 2005). As mentioned above, stratigraphic, paleobotanical, and paleozoological data show that the environment characterizing Pietrafitta at the time when the fossiliferous layers were deposited, was wet and warm with a large number of small waterbodies, streams, marshy areas, and scattered forested zones. Such a paleoenvironment was well suited for anurans like *Latonia*. The presence of abundant sympatric smaller frogs attributed to the genus *Pelophylax* at Pietrafitta suggests that the paleoenvironment had enough resources to sustain the presence of at least two anuran taxa: one adapted to live in a very broad spectrum of environments (*Latonia*) and one restricted to aquatic habitats (*Pelophylax*).

The recent discovery of the extant *L. nigriventer* in the marshy and palustrine areas of the Hula valley (Israel; Biton *et al.* 2013, 2016) confirms these hypotheses. The modern habitat of *Latonia* is characterized by a Mediterranean climate with hot and dry summers and cool rainy winters and annual rainfalls of about 600 mm (400 mm in the South, 800 mm in the North). The absence of *Rana* in the habitat populated today by *Latonia* is fully consistent with the known fossil record (including Pietrafitta) of these two taxa.

The presence of several specimens belonging to *Pelophylax* is additional evidence of the presence of permanent waterbodies in the ancient Pietrafitta basin since these animals are highly adapted to aquatic environments and usually do not move away from their specific waterbody (Böhme 2002).

Today, the "Oriental vipers" inhabit only the southeastern tip of the European continent (Sindaco *et al.* 2013). As mentioned above, during the Plio-Pleistocene transition, they experienced a shrinkage in their distribution as a consequence of the cooling of European climate (Szyndlar & Rage 2002). This group has been reported only in three Italian localities: Cava Passalacqua ("Terre Rosse", Gargano, Apulia), Zanclean; Cava Monticino (Emilia Romagna), Messinian; Moncucco Torinese (Piedmont), Messinian (Delfino 2002; Colombero *et al.* 2017). In Europe, this group is common in the fossil record from early Miocene to late Pliocene (see Szyndlar & Rage 2002) but very few fossil remains of "Oriental vipers" are known after the Pliocene in Western or Central Europe

(Blain *et al.* 2016). Some remains of "Oriental vipers" have been described from the Middle Pleistocene of two eastern Mediterranean sites, Emirkaya-2 in Turkey and from the late Pleistocene levels of Aetokremnos in Cyprus (Kessler & Venczel 1993; Venczel & Sen 1994; Bailon 1999), and of Varbeshnitsa in Bulgaria (Szyndlar 1991b). In some of these areas the "Oriental vipers" survive until today as biogeographic relics. These animals are typical of dry areas, which is in contrast with the paleoenvironmental reconstruction of the Pietrafitta site. It is possible that at least some of the surrounding areas of the ancient wetland of Pietrafitta were occupied by drier open spaces, as also suggested by the occurrence of the vole *Allophaiomys chalinei* Alcalde, Agustí & Villalta, 1981 a species well adapted to semi-arid environments (Gentili *et al.* 1996).

Our revision of the chelonian remains from Pietrafitta confirms the abundant presence of a species of the *Emys orbicularis* group, as already proposed by Kotsakis & Gregori (1985) based on other material that is not currently available to us. The Pietrafitta sample very likely belongs to the nominal species because it is the only one currently present in continental Europe. The occurrence of a minor morphological difference in the acromions from Pietrafitta compared to extant *Emys* spp. deserves further investigation. The anterior lobe of a plastron has been referred to *Testudo hermanni* and represents the first and only evidence of this taxon at Pietrafitta. All the remains of freshwater turtles belong to *Emys*, whereas *Mauremys* Gray, 1869, which is present in peninsular Italy until the Middle Pleistocene (see Chesi *et al.* 2007) and at least in some cases is associated with both *Emys orbicularis* and *Testudo hermanni* (Delfino & Bailon 2000), is absent.

CONCLUSIONS

The analysis of the ectothermic vertebrate assemblage from Pietrafitta results in the identification of a significant number of teleost, amphibian, and reptile taxa. As mentioned above, it is very likely that a large number of remains (and possibly taxa) of small vertebrates might have been lost because of the lack of systematic research during the first years of excavations. The presence of the two species of water-related anurans, *Latonia* sp. and *Pelophylax* sp., the pond turtle *Emys* gr. *E. orbicularis*, the tortoise *Testudo hermanni*, and the freshwater teleosts (*Barbus,* aff. *Squalius, Scardinius* aff. *erythrophtalmus, Tinca*) supports the paleoenvironmental reconstruction of Pietrafitta based on previously published sedimentological/ stratigraphic and paleobotanical data.

Two herpetofaunal taxa are of particular interest for their presence in Europe during the Late Villafranchian: *Latonia* sp. and *Vipera* cf. gr. "Oriental vipers". The occurrence of these animals underlines the importance of the Italian Peninsula during the Plio-Pleistocene cooling trend. The alytid frog *Latonia* was thought to have gone extinct in Europe during the first half of the Pliocene. The last surviving species is the extant *L. nigriventer* from the Pleistocene and Holocene of Israel.

The last representative of the "Oriental vipers" complex in Western-Central Europe was described by Bailon & Blain (2007) and Blain *et al.* (2016) from the late Pliocene of the Iberian Peninsula. Today, this group occurs on a narrow strip along the southern edge of Thrace and some island of the Aegean Sea (Sindaco *et al.* 2013). The presence of these two taxa in the Early Pleistocene of Central Italy is relevant to properly define the biogeographic role that the Italian Peninsula played during this period.

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